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Systematics and Biogeography of the Desert Crane Fly
Subgenus *Tipula* (*Eremotipula*) Alexander
(Diptera: Tipulidae)

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ABSTRACT—The North American desert crane fly subgenus *Tipula* (*Eremotipula*) is revised. Thirty-six species are included in the group, of which thirteen are newly described: *anasazi*, *artemisiae*, *baumanni*, *byersi*, *disspina*, *elverae*, *evalynae*, *jicarilla*, *larreae*, *maderensis*, *rogersi*, *sackeni* and *spinosa*, all from western North America. *Tipula incisa* Doane, *T. kirkwoodi* Alexander and *T. spinerecta* Alexander are transferred from the subgenus *Lunatipula* Edwards to *Eremotipula* Alexander; *T. incisa* is the only species of the subgenus found east of the Rocky Mountains. The following new synonymies are proposed: *Tipula albocincta* Doane (= *Tipula impudica* Doane), *Tipula carunculata* Alexander (= *Tipula lyrifera* Dietz), *Tipula coconino* Alexander (= *Tipula dimidiata* Dietz) and *Tipula spernata* Dietz (= *Tipula sinistra* Dietz). Lectotypes are designated for *Tipula impudica* Doane and *Tipula incisa* Doane. All species are described, the taxonomically useful structures of the male and female genitalia are illustrated, and a key to identify adults of *Eremotipula* is presented. Geographic distributions, seasonal occurrence and habitats are summarized for each species.

The phylogenetic relationships of the subgenus *Eremotipula* within the genus *Tipula*, and those of the species within *Eremotipula* were analyzed through parsimony algorithms using mostly characters of the male and female genitalia. Many of these characters have not been used previously for determining relationships. *Eremotipula* is shown to be monophyletic; its sister group is a redefined subgenus *Lunatipula* s. str. with *Lunatipula* as presently defined being polyphyletic. The *Lunatipula-Vestiplex* series of subgenera of *Tipula*, to which *Eremotipula* is included, appears to be monophyletic. The subgenera *Lunatipula* s. str., *Triplicitipula* and *Labiutipula* were used as outgroup taxa for analyzing the species relationships within *Eremotipula*. *Tipula incisa* is shown to be the sister species to the rest of the subgenus *Eremotipula*.

Nearly all species of *Eremotipula* are found in shrubby vegetation in xeric areas, such as *Artemisia* steppe or *Larrea* deserts, primarily in the Mojave and Great Basin regions. One species, *incisa*, occurs in riparian woodlands of western and central North America. Most species are endemic to the Mojave or Great Basin Deserts; few species are endemic to the Sonoran and none to the Chihuahuan Deserts. Twelve areas of endemism are outlined in western North America, with some corroboration from other insect distributions. Most species of basal lineages occur in lower elevations and in highly xeric areas, with many species of more recently derived lineages inhabiting comparatively more mesic habitats at higher elevations. Limited congruence of area relationships is seen with those outlined by Noonan (1990) and Stonedahl & Schwartz (1986) for carabid beetles and mirid bugs, respectively. *Eremotipula* possibly first evolved during the Miocene, when xeric, shrubby habitats first became available in western North America. A high proportion of sister-species pairs are found to be allopatric, possibly relating to recent speciation.

INTRODUCTION

Species of the crane fly family Tipulidae are typically found in moist environments as the larvae usually require aquatic to semi-aquatic conditions (Alexander & Byers 1981). Even species with terrestrial larvae, for example, in the genera *Nephrotoma* and *Tipula*, are usually found in mesophytic woodlands. Several groups in the vast genus *Tipula*, however, are found in semi-arid to arid habitats, including the subgenus *Eremotipula*. Most of the 36 species in *Eremotipula* are restricted to some part of western North America, with a single species occurring east of the Rocky Mountains. The greatest concentration of species is in the Great Basin and Mojave deserts, with others ranging north to British Columbia, and south to southern Arizona and northern Baja California. Species of *Tipula* (*Eremotipula*) are closely associated with open areas of xeric-adapted shrubs, such as sagebrush (*Artemisia tridentata*) stands in the Great Basin or creosote bush (*Larrea divaricata*) communities in the Mojave desert. Some areas inhabited by these flies receive as little as 116 mm (4.6 in) average precipitation per year, and experience average summer temperatures of 39° C (102° F).

All publications on the subgenus *Eremotipula* have appeared in only the last eighty years and consist mainly of isolated species descriptions accompanied by few illustrations. Aside from a few distinctive taxa, most species in the group could not be reliably identified prior to this revision. Although Alexander (1965a) commented that the subgenus was found in "semiarid regions," little was known concerning the biology of these flies apart from a few brief comments on adult habitats.

MATERIALS, METHODS, AND TERMINOLOGY

GENERAL

This study was based on approximately 2000 adult specimens of *Tipula* (*Eremotipula*). Species of *Eremotipula* are poorly represented in collections; therefore, all specimens used in this study were important to the final results. I examined material in the following 20 collections and am indebted to the curators at that time who responded to my requests for specimens. Acronyms for the collections also are listed, and used in the text.

- AMNH American Museum of Natural History, New York, New York; R. T. Schuh.
- ANSP Academy of Natural Sciences, Philadelphia, Pennsylvania; D. Azuma.
- BYU Brigham Young University, Provo, Utah; R. W. Baumann.
- CAS California Academy of Sciences, San Francisco, California; P. H. Arnaud, Jr.
- CMNH Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; C. W. Young.
- JKG Jon K. Gelhaus Collection (now part of ANSP collection).
- LACM Los Angeles County Museum of Natural History, Los Angeles, California; the late C. L. Hogue.
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; S. Shaw.
- UBC University of British Columbia, Spencer Entomological Museum, Vancouver, BC, Canada; S. G. Cannings.
- UCB University of California at Berkeley, California; G. W. Ulrich.
- UCD University of California at Davis, California; the late R. O. Schuster.
- UCM University of Colorado Museum, Boulder, Colorado; U. Lanham.
- UCR University of California at Riverside, California; S. I. Frommer.
- UIM University of Idaho, Moscow, Idaho; F. Merickel.
- UK University of Kansas, Snow Entomological Museum, Lawrence, Kansas; G. W. Byers.
- UMAA University of Michigan, Museum of Zoology, Ann Arbor, Michigan; M. F. O'Brien.
- USNM National Museum of Natural History, Smithsonian Institution, Washington, DC; W. N. Mathis.
- TAMU Texas A & M University, College Station, Texas; J. Woolley, E. Riley.
- USU Utah State University, Logan, Utah; W. J. Hanson.
- UWL University of Wyoming, Laramie, Wyoming; R. Lavigne.
- WSU Washington State University, James Entomological Collection, Pullman, Washington; R. S. Zack.

ZMUA Zoological Museum, University of Amsterdam, The Netherlands; P. Oosterbroek

Most specimens examined were mounted on points or directly pinned. Approximately 200 specimens were preserved in alcohol. Nearly all specimens I collected were papered in the field and mounted horizontally on points following the methodology described by Byers (1961). Although Brodo (1987) suggests a modified direct-pinning technique in order to permit observation of pleural setal patterns, these setae are not important in *Eremotipula* and some other groups. A modification of her technique was useful though for spreading the hypogynial valves and cerci of the female terminalia in the field, with subsequent ease of examination of the important internal ridges and patterns of the female eighth sternum (Fig. 1). Brodo's method does have the disadvantages of consuming more time and space in the field, and resulting in a specimen more prone to breakage, so I "pinned" out only representatives of the different species collected at a site, and not every female specimen. A disadvantage of papered specimens is the tendency for compressing the freshly caught fly in the envelope; this is easily prevented if the specimens are not kept tightly packed while drying.

The few specimens available in museum collections were augmented by many more obtained during a series of collecting trips in 1985–1986 (ten weeks total) and 1990–1993 (twelve weeks total), covering much of the geographic and seasonal range of the subgenus. The importance of fieldwork for understanding the species and distributions cannot be overemphasized. For example, ten weeks of fieldwork in 1985–1986 yielded nearly 20% of the specimens used in the study as of 1986 (more than were found in any museum) and 18 of the 35 species (at that time second only to the USNM in representation), conclusively showing that the paucity of specimens in museums results from a lack of effort to collect crane flies in arid areas (an admittedly unlikely place for a crane fly collector!) rather than actual rarity of the insects. I collected adults primarily by aerial netting, or at ultraviolet and white lights. Light-trapping attracted both sexes and often resulted in collections of species not found at the same site earlier in the day. Light trapping is often not useful at high elevations when night temperatures are low enough to inhibit activity. *Tipula* often does not alight on

an illuminated cloth at a light trap, and maximum collecting success is accomplished by netting flies as they come close to the lights. Adults of a few species were obtained by rearing larvae and pupae.

The species in this revision are primarily based on characters of males only (i.e., genitalia) although subtle characters in non-genitalic features (mostly wing patterning and body coloration) and genitalic morphology were found to identify most females of the subgenus. The females of twelve species remain unknown, and the males are unknown for one species. Larvae and/or pupae were reared and associated for eight species in the group but are not treated in this publication.

Descriptions of non-genitalic features (size, color, setation, etc.) are based on a detailed examination of ten specimens of each sex (if available) from throughout the range of each species. Description of the male hypopygium and female ovipositor were based on a careful examination and dissection of about five individuals (where available). Unlike non-genitalic features, the male hypopygial structures showed little significant intraspecific variation, and five specimens seemed adequate for detailed study of most species. Female ovipositor structures also seem not to show appreciable intraspecific variation, although the lack of specimens and difficulty of observation prevent a clear assessment. All specimens of a species were checked against the description, and deviations or variations were added to the text. Unless indicated otherwise, all specimens listed in the "Specimens Examined" section were studied.

An understanding of the complex structure of the male genitalia and less complicated female ovipositor only grows out of a detailed examination of cleared genitalia or alcohol-preserved specimens. Important structures such as the adminiculum, membranous lobe area between the eighth and ninth sterna, and the ventral plates of the ninth tergum of the male, and the inner ridge and associated color and structures of the eighth sternum of the female are partially to completely obscured in dried specimens. Routine identifications of the males, however, can be made from dried specimens and some female specimens have the cerci and hypogynial valves spread allowing observation of the inner ridges. Genitalia for study were cleared in hot 10% KOH (5+ minutes) or NaOH (1–4 minutes) after brushing the abdomen

(several hours previously) with soapy water. The cleared hypopygium or ovipositor was rinsed in 5% acetic acid or distilled water, and studied in water or glycerin. Genitalia were stored in glycerin in the bottom 8 mm cut from a standard 1 dram glass vial, with the vial bottoms placed in 24-well culture cluster dishes (each well 16 mm wide x 18 mm deep) or in separately labeled vials of alcohol. The genitalia are permanently stored in a genitalia vial pinned with the specimen.

Most illustrations were drawn from cleared specimens, less often from alcohol-preserved or dried specimens. Dissected parts, such as the male ninth tergum or inner dististyle, were mounted in glycerin jelly on depression slides before illustration. The majority of drawings were made using a drawing tube on a Zeiss or Wild dissecting microscope (usually 64× or less magnification) or Nikon compound microscope (50× or more). Some of the drawings were made using a grid on a Zeiss dissecting microscope.

Terminology follows for the most part that set out by McAlpine (1981), with exceptions noted elsewhere in this section. Comments here on variation refer to that among the species of *Eremotipula*, unless otherwise noted. Abbreviations used in the text are listed below; those used only for the figures are explained in the figure legends.

Adm	adminiculum
A9S	appendage of ninth sternum (Mannheims 1962)
biol	biological data
BS	basistyle
cat	listed in catalog
DL	dorsal lobes of 9T
dor	dorsal
ID	inner dististyle
lat	lateral
loc	locality information
OBL	outer basal lobe of inner dististyle
OD	outer dististyle
redesc	redescription
sp1	"spangen 1", anterodorsal part of genital bridge (Neumann 1958)
sp2	"spangen 2", mesal part of genital bridge (Neumann 1958)
STP	subtergal process of 9T
ven	ventral
VL	ventral lobes of 9T
8S	eighth sternum
9T	ninth tergum

9S	ninth sternum
# m	altitude in meters
CPA	C. P. Alexander, collector
CWY	C. W. Young, collector
GWB	G. W. Byers, collector
JKG	J. K. Gelhaus, collector
SAT	S. A. Teale, collector

EXPLANATION OF MEASUREMENTS

Body length: measured from tip of nasus to posterior edge of postgena (back of head), then pronotum to posterior edge of 9S (I excluded the neck region from body length as it can be contracted or expanded.)

Wing length: measured from base (beginning of costal vein) to wing apex.

Wing width: measured transversely across wing between A₁ and A₂.

Ratio of length 9T/BS: length measured from acrotergite to posterolateral edge of tergum, and from acrosternite to basistylar suture lobe; measured from cleared specimens and not comparable to ratios from dried specimens.

Ratio of length STP/9T: length of STP measured dorsally from where STP arises free from tergum, and to apex; length of 9T measured as above.

OBL length/width: length measured from base (dorsal emarginate area of inner dististyle posterior to crest) to apex; width is shortest distance from area of dorsal emargination to posterior margin dorsal of posterior condyle.

Membranous lobe l/w: measured from dissected eighth sternum, viewed from inner side, width measured at base.

NON-GENITALIC EXTERNAL CHARACTERS

Most non-genitalic features showed individual variation without geographic correlation, or were homogeneous among the species in the subgenus. For example, coloration and setation tended to show great intraspecific variation, with the shapes of the thoracic sclerites showing little variation. The development of a *uasus* on the rostrum has often been mentioned in generic or subgeneric descriptions, but it varied greatly within a single species of *Eremotipula*; e.g., in *diversa*, the nasus was absent to well-developed. The stripe on the dorsum of the *head* and the two pairs of stripes on the *mesothoracic notum* varied from obsolete to rather dark within a species, with the thoracic stripes sometimes interrupted near midlength.

Similar variation was seen in the spots on the postsutural scutum.

Brodo (1987) found the presence or absence of anepisternal setae to be a reliable diagnostic character. I found little variation in the setae arising between the thoracic stripes and on the scutellum and mediotergite, and much intraspecific variation in the number and color of the setae on the mesokatepisternum (e.g., in *leiocantha*, setal number varies from 0–11), meron (e.g., in *incisa*, 0–5 setae), and metakatepisternum. For these setal characters, the intraspecific variation far exceeded any differences between species. Certain setal characters do appear useful for a few species. For example, the thoracic setae of *dissipina* are long and light-colored, unlike most setae found in other species of the subgenus, with certain species (e.g., *sinistra*) having similar setae only along the posterior border of abdominal tergum I.

No interspecific variation was seen in the wing venation, and, although the color pattern of the wing sometimes is useful to distinguish species, particularly for females, these patterns are subtle, and may vary over a species range (as in *incisa*, Figs. 438–441) or show sexual dimorphism (e.g., *mitrata*). Wings in all species were viewed over a white paper background at 12 $\times$, using only indirect daylight; stronger illumination obliterated the patterns. Wings mounted in balsam also had more easily distinguishable patterns. The most distinctive pattern was the yellow seam along Cu and m-cu seen in *sinistra* (Fig. 446) and *mid-dlekauffi*, but some specimens of both these species lack these patterns. Wing venation follows the terminology followed by Alexander and others, and differs from that in McAlpine (1981) in the interpretation of m-cu, Cu, and M₄; these changes are due to convincing arguments by Byers (1988).

Abdominal coloration was also variable, particularly in the extent of dorsal and sublateral dark markings on the terga. Abdominal setae were relatively uniform in color, length and arrangement on all segments except I (see above).

GENITALIC CHARACTERS

Tangelder (1985) provides an excellent discussion of the morphology of the male and female genitalia and their function, with other useful discussions found in Byers (1961), Frommer (1963), and McAlpine (1981); I see no need for repeating much of that information here. Some male struc-

tures do require an explanation to clarify the orientation of parts and my choice of terminology.

The orientation of the dorsal lobes of the male ninth tergum (subparallel or divergent) was determined from the inner borders of the dorsal lobe. The length and width ratio of the dorsal lobes, although obviously varying among the species, was difficult to measure as the lobes have no definite boundary from the rest of the tergum.

Although the dorsolateral margin of the basistyle is always visible, the dorsomedian (inner) border is not visible in dried specimens. The appendages of the male ninth sternum are usually visible, but may be covered by long setae of the eighth sternum.

The terms dististyle and basistyle are preferred over gonocoxite and gonostylus, used by McAlpine (1981), as the latter terms imply an appendicular origin for these structures, while the former are neutral as regards to origin. The outer dististyle is always shown with the outer (lateral) side facing the reader. I could develop no useful measurement of the development of the anterior beak (= extension) of the OD, as the base wraps around the anterior side of the inner dististyle (Fig. 5) making it difficult to obtain an accurate measurement of the basal width. The length of the dorsal margin is influenced if the OD is developed anteriorly and posteriorly (e.g., *melanderiana*; Figs. 63, 349).

The orientation of the inner dististyle can cause confusion as the styles may "rest" in various positions. When they are completely in the resting position, their anterior beaks are tucked under the 9T with the outer surface dorsolateral and the inner surface ventromesal (the long setae of the outer basal lobes intermingling above the proctiger, Fig. 3). If the beaks of the ID are not tucked under the 9T, the outer side is more lateral in position, the inner side more nearly mesal (Figs. 2, 44). In any case, what I call the lateral side refers to the mostly glossy side with short dark setae extending from near the beaks to near the apex of the OBL (Fig. 4). What I call the mesal side refers to the inner side with long yellowish setae from beak to midlength and scattered over the outer basal lobe, interspersed with a patch of fine hairs (Fig. 5).

The outer basal lobe of the male dististyle presents problems in measurement and illustration. Although the illustrations (Figs. 4, 5) appear relatively two dimensional, the OBL is in most species

not so flat (Figs. 3, 6). The dorsal margin is often curved outward, markedly so in species such as *leiocantha*, where the curved area forms a shelf, and the mesal setae become nearly dorsal when the OBL is not fully in the resting position. This curvature causes problems in illustration; if the lobe is drawn at a full "lateral" view, the crest and upper beak would be distorted, and vice versa. Therefore, the apex of the OBL is described as seen in a full lateral position, although the illustration may show a slightly different aspect.

The use of the term crest (of the male inner dististyle) is restricted from that of Alexander (1965a) and Brodo (1987); further details are found under character 20 in the outgroup analysis.

The adminiculum provides many important characters for both the out- and in-group analyses, as well as good distinguishing features, but this structure is covered by the membranous proctiger and usually only visible in posterior view (Fig. 3) in dried specimens. Adminicular characters are scarcely used in the key.

The male eighth sternum can be said to have two posterior "margins"; a darkened sclerotized margin and a more distal membranous one. The membranous margin contains the setal band and lateral sclerites, and folds over on itself, connecting with the ninth sternum and bearing the membranous lobe in the invagination thus formed (Figs. 81, 241). The visibility of the membranous lobe varies with its size, extent of invagination between the eighth and ninth sterna and density of the setal band. Because of variation in invagination, the relative length of the lobe measured against the sternal setae or any other structure is not reliable.

The male intromittent organ arises at the vesica (Figs. 9, 10), extends anteriorly and then curves ventrad through a membranous pouch, eventually emerging through the dorsal spine of the adminiculum (Fig. 112). The vesica is not visible without dissection of the hypopygium. No characters were found on the vesica, but the intromittent organ does vary somewhat in length among the species.

PHYLOGENETIC ANALYSES

Two sets of analyses of relationships were carried out. First the relationships of *Eremotipula* to the other subgenera of *Tipula* (outgroup relation-

ships) were examined, then this information was used to analyze the relationships of the species of *Eremotipula* to one another (ingroup relationships). Both sets of analyses were based almost exclusively on characters of male and female terminalia, with character coding generally following the recommendations of Pimentel & Riggins (1987). Transformation series were considered linear and some were multistate. Each of the characters used in both the outgroup and species-level analyses is discussed in the following sections. The treatment of each character transformation series lists the character states, assumptions concerning homology and subsequent coding, and information from outgroup taxa regarding polarity.

Hypotheses of phylogenetic relationships were generated by analyzing the morphological character data through the parsimony algorithm in PAUP 3.1 (Swofford 1993) on a Power Macintosh 7100/66, with some analyses replicated with Hennig86, version 1.5 (Farris 1988) on the same computer with identical results. Transformation series were analyzed as non-additive (unordered) or additive (ordered). When multiple parsimonious trees were generated, characters were weighted *a posteriori* in the context of all character performance by successive approximations character weighting (SACW) (summarized by Carpenter 1988), through implementation in PAUP (Swofford & Begle 1993), then reanalyzed, and the process repeated until the trees resulting from two successive analyses were identical. Alternative topologies and character distributions were investigated through MacClade 3 (Maddison & Maddison 1992).

Because of the large number of subgenera of *Tipula* involved in this study, and the awkwardness and length of listing both generic and subgeneric names each time in the discussion, I often just list the subgeneric name without further designation. Where discussing a genus, I clearly indicate that the name is a generic, not subgeneric name. A complete list of taxa examined, with full specific designation, can be found in Table 1.

OUTGROUP ANALYSIS

Previous hypotheses of the relationships of *Tipula* (*Eremotipula*) were unavailable. At the start of the study, *Eremotipula* appeared to be monophyletic based on several features of the male gen-

Table 1. List of crane fly species among the *Vestiplex-Lunatipula* clade of *Tipula* included in the analysis of out-group relationships of the subgenus *Eremotipula*. * = type species of subgenus.

1.	<i>Tipula</i> (<i>Eremotipula</i>) <i>impudica</i> Doane *	
2.	<i>T.</i> ("Lunatipula") <i>incisa</i> Doane	(now <i>Eremotipula</i>)
3.	<i>T.</i> (<i>Hesperotipula</i>) species, near <i>chlorion</i> Alexander	
4.	<i>T.</i> (<i>Hesperotipula</i>) <i>streptocera</i> Doane *	
5.	<i>T.</i> (<i>Labiotipula</i>) <i>macrolaboides</i> Alexander	
6.	<i>T.</i> (<i>Lindnerina</i>) <i>serta</i> Loew	
7.	<i>T.</i> (<i>Lunatipula</i>) <i>aspidoptera</i> Alexander	(unplaced in spp. group)
8.	<i>T.</i> (<i>Lu.</i>) <i>atrasumma</i> Doane	(<i>atrasumma</i> group)
9.	<i>T.</i> (<i>Lu.</i>) <i>bisetosa</i> Doane	(<i>uniciuncta</i> group)
10.	<i>T.</i> (<i>Lu.</i>) <i>boregoensis</i> Alexander	(<i>boregoensis</i> group)
11.	<i>T.</i> (<i>Lu.</i>) <i>dorsinacula</i> Walker	(<i>dorsinacula</i> group)
12.	<i>T.</i> (<i>Lu.</i>) <i>duplex</i> Walker	(<i>mallochii</i> group)
13.	<i>T.</i> (<i>Lu.</i>) <i>fascipennis</i> Meigen	(<i>fascipennis</i> group)
14.	<i>T.</i> (<i>Lu.</i>) <i>flavocauda</i> Doane	(<i>tergata</i> group)
15.	<i>T.</i> (<i>Lu.</i>) <i>lunata</i> Linnaeus*	(<i>lunata</i> group)
16.	<i>T.</i> (<i>Lu.</i>) <i>translucida</i> Doane	(<i>mallochii</i> group)
17.	<i>T.</i> (<i>Lu.</i>) <i>vernalis</i> Meigen	(<i>mellea/bicornis</i> group)
18.	<i>T.</i> (<i>Lu.</i>) <i>uniciuncta</i> Doane	(<i>uniciuncta</i> group)
19.	<i>T.</i> (<i>Odonatisca</i>) sp. (cf. <i>subarctica</i> Alexander)	
20.	<i>T.</i> (<i>Pterelachisus</i>) <i>trivittata</i> Say	
21.	<i>T.</i> (<i>Serratipula</i>) <i>cyliindrata</i> Doane*	
22.	<i>T.</i> (<i>Setitipula</i>) <i>rusticola</i> Doane*	
23.	<i>T.</i> (<i>Triplicitipula</i>) <i>triplex</i> Walker*	
24.	<i>T.</i> (<i>Vestiplex</i>) <i>longiventris</i> Loew	
25.	<i>T.</i> (<i>Platytipula</i>) <i>paterifera</i> Alexander	OUTGROUP
Other species examined but not included in analysis:		
26.	<i>Holorusia hespera</i> (Arnaud and Byers)	
27.	<i>Nephrotoma ferruginea</i> (Fabricius)	
28.	<i>Prionocera</i> sp.	(Colorado)
29.	<i>Tipula</i> (<i>Eumicrotipula</i>) <i>chiricalhuensis</i> Alexander	
30.	<i>T.</i> (<i>Lunatipula</i> .) <i>cava</i> Riedel	(<i>pustulata</i> group)
31.	<i>T.</i> (<i>Lu.</i>) <i>disjuncta</i> Walker	(<i>livida</i> group)
32.	<i>T.</i> (<i>Lu.</i>) <i>rabiosa</i> Alexander	(<i>uniciuncta</i> group)
33.	<i>T.</i> (<i>Lu.</i>) <i>tergata</i> Doane	(<i>tergata</i> group)
34.	<i>T.</i> (<i>Lu.</i>) spp.	(Mexico)
35.	<i>T.</i> (<i>Tipula</i>) sp.	(England)
36.	<i>T.</i> (<i>Triplicitipula</i>) sp.	(California)
37.	<i>T.</i> (<i>Vestiplex</i>) <i>platymera</i> Walker	

italia, including the subtergal blade and extended dorsal lobes of the ninth tergum and the membranous lobe between the eighth and ninth sterna (Alexander 1965a). I began the analysis with a search for subgenera closely related to *Eremotipula* using the existing classification of the genus *Tipula* (Alexander 1965a,b). *Eremotipula*, prior to 1965, was placed in the subgenus *Lunatipula* as the *impudica* species group. It seemed likely that these

two subgenera were closely related. Likewise, several other subgenera had been split out of *Lunatipula*, and these were also considered in the analysis (Table 2). Based on larval characters, particularly the sclerotized, acute apices of the spiracular lobes, the subgenera *Vestiplex* and *Odonatisca* were considered related to at least some groups within *Lunatipula* (Theowald 1957; Savchenko 1966; Gelhaus 1986). The larvae of the subgenera

Pterelachisus and *Serratipula* show some similarity in the structure of the spiracular disc to those of *Lunatipula*, and these taxa were also included in the analysis. The subgenus *Lindnerina* shows some similarities to *Eremotipula* in the structure of the ninth tergum and Alexander (1965a) allied *Setitipula* to *Lunatipula*; both were added to the analysis. These taxa, loosely termed the "Vestiplex-*Lunatipula*" group of subgenera, and including all the old subgenus "*Lunatipula*" and part of the old "*Oreomyza*", constituted the ingroups for the analysis (Table 2). Although Theischinger & Theowald (1981) list the subgenus *Emdotipula* among the subgenera included in their *Lunatipula* s. lat., I do not consider it as closely related to any of the above subgenera, because the larva of (*Em.*) *saginata* is fully aquatic, with a morphology quite different than larvae found in any of the taxa treated here (all with terrestrial larvae, where known).

Although the total number of species included among these subgenera is over 900, only a few (2% of total) were examined in this study (Table 1). I opted to study the type species of each subgenus wherever possible; if not, I tried to examine a species that belonged to the same species group as the type species, for several subgenera are probably not monophyletic (e.g., *Lunatipula*, *Pterelachisus*). The subgenus *Lunatipula* contains over 450 described species, with tremendous diversity in the structure of the male and female ter-

minalia. For this subgenus, I selected several species, in addition to the type species, to represent that diversity. For example, I noted similarities in genitalic structure between *Tipula incisa* (placed in *Lunatipula* prior to this study) and certain species of *Eremotipula*, as well as (*Lu.*) *dorsimacula* to species of *Pterelachisus*.

Based on the preliminary nature of the composition of the ingroup for this analysis of the relationships of *Eremotipula*, the choice of a single, or even a few out-group(s) to distinguish ancestral from derived states would have been entirely arbitrary, with possibly misleading results. Instead, I examined several species in many different subgenera and genera of Tipulinae (Table 1), with the hope that a consensus could be reached concerning the ancestral states of the characters in the analysis. Added weight concerning plesiomorphic states was given to characters found in the subgenus *Platytipula*, as Savchenko (1966) considered it the most plesiomorphic subgenus of *Tipula*, and I felt confident that it was far removed from the ingroup subgenera. Additional published information on some characters was available concerning the genera *Dolichopeza* (Byers 1961), *Nephrotoma* (Oosterbroek 1980, Tangelder 1985), *Holorusia*, *Zelandotipula* and *Ischnotoma* (Vane-Wright 1967), *Prionocera* (Brodo 1987) and the subgenus *Tipula* s. str. (Neumann 1958), although many of the characters used in this analysis have not been previously studied and little relevant information can be found in the previous literature. I also considered that *Serratipula* and *Pterelachisus*, both including species with rather generalized male hypopygia, were probably far removed in relationship from *Eremotipula* and could act as functional outgroup taxa (Maddison, *et al.* 1984), although only *Platytipula* was treated as the outgroup in the final analyses.

Character Analysis

The analysis of the outgroup relationships of *Eremotipula* among the subgenera of *Tipula* was based on 36 male and 16 female genitalic characters distributed among 15 body areas, with the male ninth segment and inner dististyle contributing the most characters.

1. Male: Ninth tergum: median furrow.

0 = Ninth tergum scarcely depressed along midline, although area may be desclerotized.

Table 2. Subgenera of the genus *Tipula* included in the *Lunatipula*-*Vestiplex* complex.

Subgenus	# Species	Distribution	Pre-1966 Classification
<i>Eremotipula</i>	36*	Nearctic	<i>Lunatipula</i>
<i>Hesperotipula</i>	22**	Nearctic	<i>Hesperotipula</i>
<i>Labiotipula</i>	5**	Holarctic	<i>Lunatipula</i>
<i>Lindnerina</i>	11**	Holarctic	<i>Oreomyza</i>
<i>Lunatipula</i>	457**	Holarctic	<i>Lunatipula</i>
<i>Odonatisca</i>	9**	Holarctic	<i>Lunatipula</i>
<i>Pterelachisus</i>	184	Holarctic	<i>Oreomyza</i>
<i>Serratipula</i>	4***	Nearctic	<i>Oreomyza</i>
<i>Setitipula</i>	3***	Nearctic	<i>Lunatipula</i>
<i>Triplitipula</i>	26**	Nearctic	<i>Lunatipula</i>
<i>Vestiplex</i>	151	Holarctic	<i>Vestiplex</i>
TOTAL	908	Holarctic	

Species totals: * = this revision; ** = Theischinger & Theowald (1981); *** = Alexander (1965b & updates); others compiled from combining several sources.

1 = Ninth tergum with a median longitudinal furrow, usually furrow area slightly desclerotized (Fig. 49).

The furrow is least distinct in *Lindnerina*, but is most developed in *Eremotipula* and some species of *Lunatipula*, with the furrow usually completely bisecting the tergum. Although usually desclerotized at least anteriorly, it is sclerotized fully in (*Lu.*) *rabiosa*; the setae are short and pale, or completely absent in the furrow area. The ninth tergum in the outgroups (*Platytipula*, *Nephrotoma*) is not depressed medially; therefore, the presence of a furrow is considered derived.

Some taxa have a longitudinal pale area of desclerotization but no depression, e.g., (*Lu.*) *aspidoptera*, or a slight depression with uniform setae, e.g., *Serratipula* and *Pterelachisus*; neither condition was considered homologous to the median furrow. In *Odonatisca*, a slight transverse furrow is found near the posterior border of the tergum, but this also was not considered homologous. The character state in *Hesperotipula streptocera* is difficult to determine due to the overall reduction in the tergum; there is a pale median area but this is not clearly depressed, so a median furrow was (conservatively) considered absent.

2. Male: Ninth tergum: differentiated setae.

0 = Dorsal setae on tergum nearly uniform in size and coloration.

1 = Medial setae on tergum short and pale, lateral setae dark and elongate (Fig. 60).

Several taxa have the dorsal setae differentiated across the ninth tergum, with a contrast between the long, dark lateral setae and the extremely short, pale, medial setae. The setae in *Nephrotoma* and *Platytipula*, as well as in *Dolichopeza* (Byers 1961), *Prionocera* (Brodo 1987), and *Holorusia*, *Ischuotoma* and *Zelandotipula* (Vane-Wright 1967) are uniform in size and color across the tergum, and this must be considered plesiomorphic. The pale medial setae considered in state 1 have distinct basal sockets in the derived condition, unlike the pale, fine hairs present uniformly on the tergum in some taxa, e.g., in (*Lu.*) *dorsimacula*.

3. Male: Ninth tergum: dorsal lobes.

0 = Tergum with posterior border undifferentiated submedially.

1 = Tergum with a pair of lobes submedially, extent of lobes variable (Figs. 2, 3).

In the outgroup taxa, as well as several ingroup subgenera (*Serratipula*, *Odonatisca*), the posterior border of the tergum is at most developed laterally, with the median portion usually slightly to greatly incised. This is considered plesiomorphic. In a number of taxa, a pair of lobes is found medially, with or without a lateral development (e.g., *Eremotipula*), and this is taken as apomorphic. There is an association of the short, pale setae (2) and the dorsal lobes, in that they occur in the same region; those taxa with strongly sclerotized median points without pale setae, such as *Triplicitipula* and *Lindnerina*, were coded as plesiomorphic (i.e., lacking dorsal lobes).

4. Male: Ninth tergum: median process.

0 = Ventral plate not developed posteriorly.

1 = Ventral plate developed posteriorly into a median process (Figs. 2, 3, 234, 235).

A median process, termed here subtergal process, is found in *Eremotipula*, *Lindnerina* and *Labi-otipula* and arises from the ventral plate on the ventral surface of the tergum. The process in *Lindnerina* is strongly sclerotized, blackened and polished, while that in *Eremotipula* and *Labi-otipula* is only lightly sclerotized; the process in *Lindnerina* was not considered homologous. Since a ventral plate is absent among the outgroups (e.g., some *Prionocera* have a median process but lack any evidence of a ventral plate; Brodo 1987), and a process is absent from the basal ingroups, the presence of a process is considered derived.

5. Male: Ninth tergum: ventral plate.

0 = Ventral surface of tergum membranous or with slight sclerites only along posterior edge.

1 = Ventral surface of tergum with broad sclerite (= plate) (Figs. 234, 235).

Nephrotoma, *Tipula* (*Trichotipula*), *Prionocera* and *Scamboneura* all lack an extensive ventral sclerotized plate on the ninth tergum and have, at most, narrow bordering sclerites (Tangelder 1985: figs. 11–19). In addition, I do not see such sclerotization in *Holorusia* or *Tipula* (*Ennicrotipula*). The subgenus *Platytipula* does have a plate that is sclerotized posteriorly, and a broad plate is seen in all ingroup taxa except *Vestiplex*. Since a plate is lacking in nearly all outgroups, I consider its presence as derived.

The ninth tergum in (*Lunatipula*) *atrasumina* is highly modified, and the ventral plate is not clearly present; this state is coded "?".

6. Male: Ninth tergum: ventral plate shelf.

0 = Ventral plate, if present, relatively flat.

1 = Ventral plate with lateral edges curled inward, forming a broad shelf (Figs. 54, 235).

The ventral plate shelf is found only in *Eremotipula* (including *E.* *incisa*) and is a synapomorphy for this subgenus (see discussion of *Eremotipula* cladogram).

7. Male: Ninth tergum: ventral plate with thickened band.

0 = Ventral plate with unmodified anterior edge.

1 = Ventral plate with dark, thickened band along anterior edge (Fig. 248).

Most of the ingroup taxa with a ventral plate also have a band in some form along the edge of the plate between the anterior processes. The band is distinct in *Serratipula* but is usually faint and indistinct (e.g., in *Odonatisca*, *Eremotipula*). Although I consider the presence of the band apomorphic, it may be a symplesiomorphy at this level, pending a final determination of the distribution of the ventral plate (see discussion of outgroup cladogram).

8. Male: Ninth tergum: ventral plate with anterior processes.

0 = Ventral plate rounded anteriorly.

1 = Ventral plate with a pair of anterior processes (Fig. 61).

No processes from the ventral plate are seen in *Platytipula*, and the other outgroups lack the plate. The anterior processes are absent in *Serratipula* and *Lindnerina*, but short (*Triplicitipula*) to elongate (*Tipula dorsimacula*) in most ingroup taxa; presence of processes is considered apomorphic. The processes are twisted in *Eremotipula* (Fig. 384) and also (*Lu.*) *rabiosa*.

In *Eremotipula*, the processes are strongly attached to the sp2 sclerite, but this is not true of all other ingroup taxa. Some groups have the processes embedded in the membrane of the proctiger (e.g., *Pterelachisus*), while in others they appear free of the membrane (e.g., *Labiotipula*). The processes appear to articulate with the sclerotized rods of the proctiger when present (e.g., *Triplicitipula*). The processes in *Setitipula* are pale and difficult to distinguish.

9. Male: Ninth tergum: ventral plate extension.

0 = Anterior border of ventral plate without a small, anterolateral extension.

1 = Anterior border of plate with small pointed anterolateral extension.

The small extensions occur posterolateral to the much more conspicuous anterior processes. This development of the border is seen only in (*Lu.*) *translucida* and the (*Lu.*) *tergata* species group, and is presumed derived.

10. Male: Basistyle: dorsomedial closure.

0 = Basistyle with dorsomedian surface mostly membranous, with inner margin of "basistylar socket" incomplete, sp2 present.

1 = Dorsomedian surface of basistyle with isolated sclerite between sp2 and posterior border.

2 = Dorsomedian surface of basistyle sclerotized, forming a complete ring or socket dorsally (Fig. 226).

3 = Dorsomedian surface of basistyle completely membranous, sp2 absent or not recognizable.

The dorsomedian surface of the basistyle and the interrelated genital bridge (Dobrotworsky 1968; = sp1+sp2 of Neumann 1958) are surprisingly diverse among the Tipulinae. The entire medial surface of the basistyle is sclerotized in *Dolichopeza* (Byers 1961: figs. 17, 27), i.e. there is complete fusion of sp1, sp2 and basistyle. In *Holorusia*, the basistylar socket is completely sclerotized dorsally, with a broad band (sp1) extending ventrally; the remainder of the median surface of the basistyle is membranous. In *Platytipula*, *Odonatisca* and (*Lu.*) *dorsimacula*, the inner part of the socket is not fully sclerotized (state 0), and an isolated sclerite nearly completes the socket in *Lindnerina* and others with sp1 usually narrow (state 1). The socket is narrowly complete in several groups, including *Eremotipula* and the outgroup *Nephrotoma*, and sp1 is narrow, reduced or absent (state 2). This latter condition is unlike that in *Holorusia* and represents a separate character state. In *Hesperotipula*, the dorsomedian sclerotization is completely lost, including sp2 (state 3).

11. Male: Genital bridge fusion.

0 = sclerites of sp1 and sp2 closely approximated, with sp1 at or near the level of sp2.

1 = sp1 and sp2 not approximated, with arms of sp1 reduced in length and separated from sp2 (Fig. 226).

There is a diversity of structure in the sp1 and sp2 sclerites, or patterns of fusion ("complete bridge", Tangelder 1985). Among the ingroup subgenera in the analysis, none could be consid-

ered to have a complete, solidly fused bridge in the sense of *Holorusia*. Therefore, I question the inclusion by Tangelder (1985: 146) of the subgenera *Lunatipula*, *Vestiplex*, *Platytipula* and even *Tipula* s. s. among those taxa with complete bridges. In *Serratipula* and *Lindnerina*, sp1 and sp2 are closely approximated, but an unsclerotized zone occurs between the two sclerites, with further reduction seen in *Lunatipula* and others. The sp1 sclerite is much reduced in several groups, including *Eremotipula* and *Triplicitipula*, with a wide membranous separation between sp2 and the shortened arms of sp1 (Figs. 11, 195). Based on the long arms of sp1 seen in *Platytipula* and other basal taxa, a small or reduced sp1 is considered derived. The sp2 sclerite also varies somewhat in morphology, and in addition was not recognizable in several groups, including the subgenus *Hesperotipula* and (*Lu.*) *boregoensis*.

12. Male: Ninth sternum: anterior acrosternite margin.

0 = Acrosternite a simple dark band.

1 = Acrosternite bilobed midventrally, lobes directed anteriorly.

2 = As in 1, but lobes reflexed posteriorly.

3 = As in 2, but lobes reduced.

A simple acrosternite is found in several groups distantly related to *Eremotipula*, including the outgroup *Platytipula*. The subgenera *Vestiplex* and *Lindnerina*, as well as (*Lunatipula*) *atrasumma* have the midventral portion strongly bilobed, approximately as in the subgenus *Tipula* (Tangelder 1985: fig. 20). Apparently, these lobes are reflexed in several other subgenera, strongly so in *Triplicitipula*, reduced in *Lunatipula* s. str. and *Eremotipula*. The lateral sclerites of the eighth sternum are attached, in part, to the reflexed lobes in (*Lu.*) *lunata* and (*Er.*) *incisa*. The condition in *Hesperotipula* is possibly highly derived, and might be homologous to the reflexed lobe condition (state 2). In addition, several species of *Lunatipula* have additional plates and lobes along the acrotergite which were not considered here but probably are of some use for understanding relationships at the species-group level.

The following is a general discussion of characters 13–15, appendages of the male ninth sternum. Frommer (1963) termed the posterior lobes of the ninth sternum "fragmenta" (after Rees & Ferris 1939) and noted their occurrence in three distantly related subgenera of *Tipula*: *Beringoti-*

pula, *Lunatipula* and *Platytipula*. Regarding this feature in *Lunatipula* s. lat., Frommer rightly states (1963: 578): "The presence of fragmenta in the ninth sternum in the species of *Lunatipula* has enabled me, so far, to recognize all species in this subgenus on sight by this character alone." An equivalent term in use for the homologous appendages found only in *Lunatipula* and allies is "appendages of the ninth sternum," A9S (Mannheims 1963: 138, Anhangen des 9 sternite). This term and its abbreviation is used here.

Small to large lobes or slightly smaller sclerites, set off from the rest of the sternum by membrane, are seen in all the ingroup taxa considered in this analysis, but are not seen in *Platytipula* and non-*Tipula* species examined (Table 1; see also character 13). In *Vestiplex*, *Serratipula* and others, this area remains simply a sclerite with few setae, but most other ingroup taxa actually have a lobe with a free distal portion (character 14). In some groups placed as derived by the analysis, such as *Eremotipula*, the distal portion actually becomes differentiated and constricted from the basal portion (Fig. 2). I have called the basal portion "dorsal lobe" and the distal portion "ventral lobe" (character 15), to reflect the fact that the ventral lobes, at least, hang downward from near the base of the adminiculum. The dorsally-directed lobes in the subgenus *Odonatisca* may not be homologous with the lobes considered here, and this area is not clearly separated by membrane from the sternum in that subgenus.

13. Male: A9S development.

0 = Lobes present or absent, but no swollen sclerite separated by membrane from rest of sternum.

1 = A swollen sclerite distinctly separated from remainder of sternum by membrane.

Although *Platytipula* has lobes on the ninth sternum, they are not separated from the rest of the sternum and are not considered homologous. The corresponding areas of *Nephrotoma*, *Holorusia* and *Tipula* (T.) are flat and undifferentiated, although the areas in *Holorusia* are delimited from the sternum by membrane. All these conditions are considered plesiomorphic, with the development of a swollen sclerite or lobe, clearly separated from the sternum, considered derived.

This feature appears as a synapomorphy for all the subgenera in the *Vestiplex-Lunatipula* series, although this may be inclusive of additional groups when they are examined.

14. Male: A9S free distally.

0 = A9S area a simple swollen sclerite, with no free lobe.

1 = A9S a free lobe distally (Fig. 2).

The development of this area in some subgenera such as *Serratipula* and *Pterelachisus* consists of a slightly swollen sclerite with some setae. Most groups possess a single pair of short (*Labiopipula*) to long (*Lindnerina*) lobes, and this is derived; the lobes are reduced in some species of *Lunatipula* (*flavocauda*), and divided in others (*rabiosa*). The development of a distally free lobe occurs in most of the ingroup taxa.

15. Male: A9S constricted.

0 = A9S evenly narrowed to apex, rarely gradually expanded apically.

1 = A9S abruptly narrowed subapically, with a slightly to greatly expanded apical portion (Fig. 92).

State 1 is considered derived, for a distal constriction of the A9S is not seen in the functional out-groups. In *Eremotipula* and other groups, the A9S is constricted subapically with the basal and apical portions clearly delimited; often the apical lobe has specialized setae as well (see characters 16–17). State 1 is seen in (*Lu.*) *lunata* but not in most of the other species of *Lunatipula* that were examined.

16. Male: A9S: setal character I.

0 = A9S lobes or area with long setae throughout.

1 = A9S lobes with setae of the distal region differing in size, thickness and placement from proximal setae (Fig. 342).

Character 16 shows approximately the same distribution among taxa as character 14, also a feature of the appendage of the ninth sternum. State 1 is considered apomorphic as state 0 occurs among the functional out-groups, *Pterelachisus* and *Serratipula*.

17. Male: A9S: setal character II.

0 = Distal setae of A9S straight.

1 = Distal setae of A9S twisted in apical half (Fig. 44).

The setae in several subgenera, including *Triplicitipula* are extensively twisted or spiraled, although these are difficult to observe in the subgenera *Hesperotipula* and *Labiopipula*. Within *Eremotipula*, *incisa* has spiral setae (Fig. 44), but the

rest of the species do not (Fig. 62), and in *Lunatipula*, spiral setae are seen in the type species, *lunata*, but not in any other species examined.

18. Male: Inner dististyle: area above upper beak shelf-like.

0 = Area above upper beak not distinguishable as a flattened shelf.

1 = Area above upper beak a flattened shelf (Fig. 6).

The condition in *Vestiplex* resembles that in *Platytipula*, the genus *Prionocera* and other outgroups with the area above the beak ridge-like and scarcely expanded. In nearly all the ingroups examined except *Vestiplex*, the area above the upper beak is flattened and expanded, and this (state 1) is considered derived.

19. Male: Inner dististyle: upper beak with striae.

0 = Shelf of upper beak smooth, or with fine wrinkles.

1 = Shelf of upper beak with distinct, longitudinal or transverse, striae (Fig. 6).

The area above the upper beak is generally smooth or at most with fine wrinkles among the subgenus *Platytipula* and non-*Tipula* examined, as well as in the functional outgroups *Serratipula* and *Pterelachisus* and this is thought to be the plesiomorphic condition. The remaining ingroup taxa have this same region of the dististyle with numerous, distinct striae, often subparallel, and this is considered apomorphic. The condition in *Odonatisca* is doubtfully homologous, as the striae are few in number and transverse unlike those seen in the other taxa.

20. Male: Inner dististyle: crest.

0 = Dorsolateral surface of upper beak not developed into a crest.

1 = Dorsolateral surface of upper beak extended into flat, lightly sclerotized or membranous crest (Figs. 5, 64).

A crest is determined in this work to be a development of a flat, often membranous plate along the dorsolateral margin of the beak, and contrasting with the upper surface of the beak by lacking the hairs and striae. The lateral surface of the crest is usually sculptured. This description is compatible with that given by Alexander (1965a): "... a thin plate or blade", but contrasts sharply with that given by Brodo (1987) in which the term just indicates the unmodified dorsal area

of the inner dististyle that lies posterior to the beak.

A crest is not present in most of the ingroup subgenera examined here, nor in most of the outgroup taxa, except for the genus *Nephrotoma*. *Lindnerina* and (*Lunatipula*) *boregoensis* have a narrow plate along the upper surface, with the lateral surface striate, but these plates are scarcely distinct from the upper shelf, and they are not thought to be homologous. Crests are only seen among the ingroup taxa in *Eremotipula* and some of the species of *Lunatipula* (including *lunata*) where the crests are distinct from the upper shelf and arise from the lateral surface of the beak. Within *Eremotipula*, the crest is membranous in most species groups (Fig. 5), but apparently lost in the *eurystyla* species group (Fig. 90). Among the species examined in *Lunatipula* s. str., only (*Lu.*) *translucida* lacks the crest, but even in this species the lateral area of the dististyle, where the crest would be expected to arise, is tuberculate.

A crest was not seen in the type species of *Hesperotipula*, *streptocera*, examined here but is seen in *chliron* and figured for *californica* (Alexander 1965a: fig. 12).

21. *Male: Inner dististyle: basiconic pegs.*

0 = Basiconic pegs absent from inner dististyle.

1 = Basiconic pegs present.

22. *Male: Inner dististyle: grouped basiconic pegs.*

0 = Basiconic pegs few in number, not placed together in a group.

1 = Basiconic pegs placed in close, oval to circular grouping (Figs. 5, 6).

Basiconic pegs or sensilla are found in the subgenus *Tipula* among the outgroups, and in the functional outgroup *Serratipula* and many of the other ingroup subgenera in the analysis, including *Eremotipula*. In (*Tipula*) *paludosa*, the pegs are in a band extending along the outer basal lobe of the inner dististyle. In the other subgenera (all ingroup taxa) which possess pegs, the sensilla are usually in a tight, often circular or oval, group near the base of the outer basal lobe.

The absence of basiconic pegs in most outgroup taxa examined leads me to consider their presence as apomorphic, regardless of the scattered pegs found in the subgenus *Tipula*. Likewise, the absence of grouped pegs in the subgenus *Tipula* and the functional outgroup subgenera such as *Ser-*

ratipula indicates that the grouping of pegs is a derived feature.

Alexander (1965a) states that pegs occur in (*Platytipula*) *moiwana*, but I see only sensory pores on the dististyle in the related species *paterifera*. Pegs are absent in several groups such as *Hesperotipula* and *Triplicitipula* (although they are illustrated for (*Tr.*) *doanciana*, Alexander 1967: fig. 229). The assertion by Alexander (1965a) that the placement of the basiconic pegs allows recognition of the outer basal lobe of the inner dististyle (especially when the lobe is highly modified) is discussed under character 23.

23. *Male: Inner dististyle: outer basal lobe.*

0 = Inner dististyle without development of a posterior lobe.

1 = Inner dististyle with outer basal lobe present posteriorly (Fig. 6).

Alexander (1965a) considered the outer basal lobe to occur in most groups of *Tipula*, but the diversity of structure seen among the subgenera makes me question whether all these types of lobes are homologous. The outer basal lobe is absent from the species of *Platytipula* and *Vestiplex* I examined (cf. Alexander 1965a: figs. 20, 32), as well as from the genera *Nephrotoma* (Tangelder 1985), *Prionocera* (Brodo 1987) and *Dolichopeza* (Byers 1961). Alexander (1965a) states that the sensory (= basiconic) pegs are of "considerable importance in determining the location of this lobe when it has become complex or highly modified in structure," but actually few subgenera have these pegs (see characters 21–22). Likewise, the presence of a patch of fine setae (character 24) is a good indication, but this feature is restricted to even fewer groups.

Among the ingroup taxa, the outer basal lobe is absent from *Vestiplex* and (*Lunatipula*) *atrasumma*, and probably also from *Hesperotipula* and *Triplicitipula*. The latter two subgenera have posterior lobes on the inner dististyle, but these lobes lack both pegs and the fine hair patch, and are possibly not homologous to the lobes in other subgenera. The presence of an outer basal lobe is considered here derived within the ingroup for this analysis, but it is possible that this is a character of most of *Tipula* species, as proposed by Alexander.

24. *Male: Inner dististyle: patch of fine hairs.*

0 = Mesal surface of outer basal lobe with only long setae present.

1 = Mesal surface with long setae and a patch of fine, medium-length hairs (Fig. 5).

Nearly all the species of *Eremotipula* and some of *Lunatipula* have a patch of fine yellow hairs near the base on the mesal surface of the outer basal lobe; these are sometimes hard to distinguish from the longer, abundant yellow setae. State 1 must be considered apomorphic, as this hair patch is absent from all the outgroup taxa and most of the ingroups.

No specific mention of this feature is found in previous works, although Alexander illustrated the hairs many times (e.g., Alexander 1946a: fig. 7, 1967: fig. 85).

25. Male: Inner dististyle: pilosity of outer basal lobe.

0 = Outer basal lobe covered with short hair, not smooth and glossy.

1 = Outer basal lobe smooth and glossy, without short pile, although patch of long hairs may be present (Fig. 4).

The lobes in the functional outgroups (*Pterelachisus* and *Serratipula*), have at least some areas of short hair, giving a fuzzy appearance, and the lobe itself is often thick. In most of the ingroup taxa examined (except (*Lunatipula*) *aspidoptera*), the short hair is lost, and the surface is usually shiny; in addition, the lobe is often rather compressed.

26. Male: Adminiculum: dorsal spine.

0 = Adminiculum mostly membranous dorsally, without a spine.

1 = Adminiculum with sclerotized dorsal spine (Figs. 7, 8).

In most outgroup taxa, the adminiculum is essentially a simple conical structure through which the intromittent organ emerges and is guided into the female bursa copulatrix (e.g., genera *Dolichocheza*, *Prionocera* and *Platytipula*). This simple adminiculum is also seen in *Pterelachisus*, *Serratipula* and *Vestiplex* and is considered plesiomorphic. In most of the *Vestiplex-Lunatipula* groups, the apex of the adminiculum is differentiated into a median (posterior) lobe (see also character 27) and a dorsal spine, with the intromittent organ emerging through the spine. The spine is similar in most taxa that possess it and is easily recognized by reference to where the intromittent organ emerges.

27. Male: Adminiculum: median lobe.

0 = Median lobe not developed, or usually small and fully sclerotized.

1 = Median lobe expanded and mostly pale, with dark sclerotization along border (Figs. 7, 8).

The median lobe is apparently unique to a group of taxa within the *Vestiplex-Lunatipula* group of subgenera, as the lobe is absent from the functional outgroup taxa, such as *Vestiplex* and *Pterelachisus*, as well as the other outgroups. The median lobe in some subgenera is fully sclerotized and small, shaped somewhat like a hook, e.g., *Lindnerina* and *Labiotipula*. In *Eremotipula* and *Lunatipula* s. str., the median lobe is expanded dorsoventrally and membranous overall, except for a dark band along the posterior border (Fig. 304). The expanded median lobe is here considered apomorphic. This apomorphic condition is further modified in certain species, such as (*Lu.*) *lunata*, with dorsal hooks, or (*Lu.*) *tergata*, where the median lobe is a large hook (cf. closely related *flavocauda* which has an expanded median lobe). The median lobes in (*Lu.*) *translucida* and *rabiosa* are small, with sclerotization and shape similar to that in *Labiotipula*.

The condition of the median lobe in *Triplicitipula* is puzzling. The dorsal spine is present, but the median lobe is absent, or present as a pair of widely separated sclerotized arms (Alexander 1967: figs. 226, 229).

28. Male: Adminiculum: lateral plates.

0 = Adminiculum without lateral plates.

1 = Adminiculum with closely attached lateral plates, apices free and often rounded (Figs. 7, 8).

2 = As in 1, but plates are curved hooks, mostly free from body of adminiculum.

Lateral plates are restricted to the subgenera *Eremotipula* and *Lunatipula* s. str. There are no lateral modifications of the adminicular body in the other ingroup subgenera. Whether the lateral plates in these two subgenera are homologous is unclear from the few taxa examined in this study. *Tipula incisa*, the most basal species of *Eremotipula*, has three lateral plates on each side (Fig. 47). These are presumably fused together in all other species of *Eremotipula* (Fig. 78), but three plates may also be an autapomorphy of *incisa*. I see no intermediate conditions between the plates in *Eremotipula* and some *Lunatipula* (*lunata* and allies), and they may not be homologous.

29. Male: Adminiculum: sclerotized basal plate.

0 = Base of adminiculum bisected by a large membranous area, each side extended and attached to the surrounding membrane by a "foot,"

with body of adminiculum mostly free from sternum (Fig. 7).

1 = Base of adminiculum expanded laterally as large sclerite, usually with narrow membranous field, each "foot" short, or unrecognizable, body of adminiculum broadly attached to membrane.

The adminiculum in most ingroup taxa is relatively narrow, the base not extensive or expanded. The base of the adminiculum in species of *Lunatipula* (*lunata* and allies) is a broad sclerite and is considered apomorphic. Character 29 may provide strong support for a monophyletic *Lunatipula* as defined narrowly around *lunata*. The adminiculum in (*Lu.*) *rabiosa* is extensively desclerotized, but the configuration of the remaining sclerites shows that this is a modification from the condition detailed in state 1 above. *Eremotipula* has the plesiomorphic condition.

30. Male: Eighth sternum: shape.

0 = Sternum laterally convex and rounded, with greatest transverse width near mid-length or in apical half of sclerite.

1 = Sternum concave laterally or gradually narrowing from base to apex (greatest transverse width across basal half of sclerite) (Figs. 67, 421).

The eighth sternum in the examined outgroup taxa is broadly convex laterally (e.g., *Platytipula*, *Prionocera*, *Eumicrotipula*), and in *Holorusia* it is rectangular. In *Eremotipula*, *Lunatipula* (*lunata* and allies) and several other subgenera, the greatest width of the sternum has shifted toward the base, and the sclerite usually is strongly narrowed apically. This narrowing of the sternum appears apomorphic, although it is seen as well in the outgroup subgenus *Tipula* s. s. and the ingroup (*Lu.*) *dorsimacula*.

31. Male: Eighth sternum: anterolateral corner.

0 = Anterolateral corner of sternum not produced.

1 = Anterolateral corner produced into a distinct, rounded lobe.

State 1 is restricted to some species in *Lunatipula* (*lunata* and allies) and is considered derived. It may prove to be a useful character in the future for relating species groups within this enormous subgenus.

32. Male: Eighth sternum: apical setae.

0 = Apex of eighth sternum without setae.

1 = Membranous apical region of sternum with distinct, elongate setae (Fig. 421).

Various structures occur at the apex of the eighth sternum, but generally, among the outgroups and primitive ingroups, these do not include long setae, e.g., genera *Prionocera*, *Holorusia*, and *Dolichocheza* and subgenus *Platytipula*. Some species of the genus *Nephrotoma* species have long setae on the eighth sternum, but this is derived within the genus (Tangelder 1985: 143). Among most of the ingroup taxa, the eighth sternum has apical setae, either as a transverse band (*Setitipula*, *Eremotipula*) or as paired patches (*Triplicitipula*, (*Lu.*) *flavocauda*), or on articulated lobes (*Hesperotipula*). This is considered apomorphic. The homology of these various configurations of setae is uncertain at this level, although specific arrangements of setae are probably homologous for less-inclusive groups.

33. Male: Eighth sternum: grouped apical setae.

0 = Eighth sternum with apical setae arranged in a row (as in Fig. 240).

1 = Eighth sternum with apical setae in two, convergent, submedial groups (Fig. 67).

A complete row of setae along the posterior margin of the eighth sternum is found in taxa such as *Setitipula*, (*Lu.*) *boregoensis* and *Labiotipula*. The restriction of the setae to paired submedial setal groups is found in *Triplicitipula*, *Lunatipula* (*lunata* and allies) and *Eremotipula*. Within *Eremotipula*, however, paired groups of setae are found only in a few species (*incisa*, *melanderiana*, Fig. 67), with most showing a complete band (Fig. 240). The medial groups are completely lost in some species of *Lunatipula* s. str. (e.g., *rabiosa*). In light of these modifications, many more species will need to be studied to determine the true phylogenetic significance of this character.

The character state in *Hesperotipula* is impossible to determine as all the setae are located on a pair of lobes; this taxon is coded as "data missing".

34. Male: Eighth sternum: lateral sclerite.

0 = Apical setae of sternum undifferentiated.

1 = Some apical setae differentiated and/or isolated laterally, usually occurring on a separate sclerite (Figs. 67, 81).

An undifferentiated setal band is found only in *Setitipula* and (*Lu.*) *boregoensis*. State 1 is found in a large group of subgenera, including *Eremotipula*. Lateral setae on sclerites are lost in some species of *Eremotipula* (e.g., *diversa* species group) and probably in some species of *Lunatipula* (*flavocauda*).

35. Male: Eighth sternum: thickening of lateral setae.

0 = No setae in lateral groups particularly thickened or modified.

1 = One or more lateral setae thickened or modified (Figs. 67, 113).

The distribution of state 1 among the ingroups closely follows that for the derived state of character 34, although a wider examination of taxa may find more basal groups which have isolated lateral setae that are not thickened. Within *Eremotipula*, thickened setae are found in some species.

36. Male: Intromittent organ.

0 = Intromittent organ short, often thick, not curving cephalad from vesica farther than anterior edge of abdominal segment 8.

1 = Intromittent organ long, usually slender, curving cephalad at least into abdominal segment 7, usually farther.

The conclusion by Oosterbroek (1980), Tangelder (1985) and others that a short, thick intromittent organ is plesiomorphic is corroborated by my observations. All of the basal ingroup subgenera (*Serratipula*, *Pterelachisus*, *Vestiplex*), as well as the outgroups (e.g., subgenus *Platytipula*, genera *Holorusia*, *Prionocera*) have short organs, and this is considered plesiomorphic. The absolute length of the organ was not conducive to splitting into further states. For example, within *Eremotipula*, the intromittent organ may extend anteriorly to segment 6 in one species and all the way into the thorax in another, with no overall trend in lengthening. Tangelder (1985) points out that a lengthening (or an extension anteriorly) of the organ has occurred independently in several groups of Tipulinae.

37. Female: Eighth tergum: posterior margin 1.

0 = posterior border of female 8T straight to shallowly emarginate.

1 = posterior border of female 8T deeply emarginate, in cases nearly bisected.

Although the eighth tergum in female Tipulinae is characterized as being unmodified (Frommer 1963, Tangelder 1985), several subgenera within the *Vestiplex-Lunatipula* group have the eighth tergum with a strongly emarginate posterior border, with the tergum nearly bisected in *Serratipula* and *Vestiplex* (e.g. Savchenko 1964: fig. 162). This margin is straight or only slightly emarginate in all other Tipulinae examined.

38. Female: Eighth tergum: posterior margin 2.

0 = Posterior border of female 8T unmodified.

1 = Posterior border of 8T with a small projection medially.

A median convexity is noted along the posterior margin of the eighth tergum in numerous groups of the *Vestiplex-Lunatipula* series, including *Eremotipula*. I note a similar margin elsewhere in figures of the distantly related tipuline subgenus *Leptotarsus* (*Phymatopsis*) (Dobrotworsky 1968: fig. 19c).

39. Female: Ninth tergum: length.

0 = Female 9T length one third to one half length of 8T.

1 = Female 9T strap-like, length less than one third length of 8T.

As noted by Tangelder (1985) and confirmed in this study, the ninth tergum is "usually more or less reduced in size" among the Tipulinae. In *Vestiplex*, *Serratipula* and *Odonatisca* among the Tipulinae examined, and scattered among the Limoniinae and Cylindrotominae, the ninth tergum is extremely reduced in length (longitudinally).

40. Female: Terga 9 and 10: fusion 1.

0 = Female 9T distinctly separated by membrane from 10T.

1 = Female 9T closely associated and partially or completely fused with 10T, although boundary may be distinct.

41. Female: Terga 9 and 10: fusion 2.

0 = Female 9T separate or partially fused with 10T.

1 = 9T and 10T completely fused, no boundary indicated (except color or microtomentum)

The *Lunatipula-Vestiplex* subgenera show a tendency for fusion of the ninth and tenth terga, with complete fusion (character 41) seen in *Vestiplex*, *Odonatisca* and *Lunatipula atrasnumma*. Partial fusion (character 40) is difficult to determine, with the terga closely appressed but a boundary line still evident. Other taxa showing complete fusion are in eriopterine crane flies, such as the genera *Eriocouopa* (Stary 1976: fig. 13) and *Molophilus* (Stary 1968: figs. 4, 5).

42. Female: Tenth tergum: setae.

0 = Female 10T with conspicuous long setae (or setae similar to those on anterior terga) generally distributed dorsally.

1 = 10T with few or no setae, setae short, pale and posterolateral.

The absence of long setae on the tenth tergum (with the few setae which are present being minute and pale) is seen in most Tipulinae examined or illustrated, and stands as a possible synapomorphy for most of the subfamily. All Limoniinae and a few Tipulinae examined or figured (e.g., genus *Leptotarsus*, Young & Gelhaus 1992: fig 10; *Platytipula*, Gelhaus 1986: fig. 12) have long setae on the tenth tergum. Some taxa in the study were difficult to code as the abdomen in general had no setae (e.g., *Lunatipula dorsimacula*, *Serratipula*) or with a few long setae on the tenth tergum (*Hesperotipula streptocera*). Within the ingroup, the state coded 1 is probably a symplesiomorphy.

43. *Female: Tenth tergum: posteromedial margin.*

0 = Posterior border of 10T truncate or with elongate, narrow median point, length one-third or more length of 10T.

1 = Posterior border of 10T with much shorter, median point, length one-third or less length of 10T, or point broad.

The posterior border of the tenth tergum forms a long or short point in Tipulinae and Cylindrotominae (e.g. cylindrotomine genus *Liogma*, Peus 1952) and may be a synapomorphy for the two groups. No point is seen in any Limoniinae examined, and the margin is straight, emarginate or convexly rounded. This point has been postulated to be the remnant of the eleventh tergum (Crampton 1942: 81, Byers 1961: 693) and termed the supraanale by Tjeder (1958: 134). Crampton (1942: fig. 9A) and Dobrotworsky (1968: fig. 5A) even show this area as the "eleventh tergum" clearly divided by a line from the tenth tergum in the tipuline genus *Clytocosmus*. The point is extended among many Tipulinae, including *Tipula* (*Platytipula*) (Gelhaus 1986: fig. 10) but short among many taxa of the *Vestiplex-Lunatipula* groups, including *Eremotipula*.

44. *Female: Tenth tergum: apodeme.*

0 = 10T with longitudinal apodeme.

1 = 10T without longitudinal apodeme

Frommer (1963) states "The most conspicuous modification in the . . . tenth tergum is the median longitudinal inflection (Frommer 1963: figs. 68, 69, 71) to which powerful muscles that move the cerci are attached." The presence of a longitudinal

apodeme is probably a synapomorphy for most or all Tipulinae, since it appears lacking in other crane flies, but is also not seen in certain Tipulinae examined, such as the genus *Leptotarsus* (Young & Gelhaus 1992) and *Tipula* (*Yamatotipula*) *novarae*. Within the ingroup, the apodeme is lacking from certain *Lunatipula* and *Hesperotipula streptocera*, all with reduced cerci.

45. *Female: Tenth tergum: posterior border.*

0 = Posterior border of 10T unmodified laterally.

1 = Posterior border of 10T with protuberance laterally

Similar, low protuberances are seen laterally along the posterior margin of the tenth tergum in both *Tipula* (*Lunatipula*) *boregoensis* and *T. (Hesperotipula)* *chlorion*.

46. *Female: Cerci: size.*

0 = Cerci blade-like, elongate, with apex slightly to strongly narrowed from base.

1 = Cerci short with apex rounded

Elongate, blade-like, well sclerotized cerci are characteristic of crane flies (McAlpine 1981). Although often modified in *Lunatipula*, particularly shortened, they often retain the narrowed apex (e.g., *Lunatipula vernalis*). Short cerci with rounded apices are seen in *Hesperotipula streptocera* and *Lunatipula atrasumma* among the ingroup taxa examined here, a condition seen elsewhere in other Tipulinae (e.g., genus *Leptotarsus*, Dobrotworsky 1968: fig. 5B) and eriopterine Limoniinae (e.g., *Gonomyia*, Stary 1970: figs. 3, 7).

47. *Female: Cerci: edge.*

0 = Ventrolateral edge of cerci unmodified.

1 = Ventrolateral edge of cerci expanded, with roughened or toothed margin

The vast majority of crane flies have smooth margins along the ventrolateral edge of the cerci, as seen in the outgroup taxa examined for this analysis (*Platytipula* and others) and most species of *Eremotipula*, and is considered plesiomorphic. Several groups have cerci with toothed margins, as in some *Tipula* (*Vestiplex*) (Alexander 1918: fig. 43; Savchenko 1964: figs. 96, 147, 162) and the limoniine genus *Phyllolabis* (Alexander 1967: fig. 342A-F), or the margin roughened or irregular, as in *Serratipula*, *Odonatisca* and the *Eremotipula eurystylis*-species group (Figs. 99, 128).

48. *Female: Cerci: dorsum.*

0 = Dorsal surface of cerci narrowly flat or slightly rounded.

1 = Dorsal surface of cerci broad and flat, giving cerci appearance of being distinctly three sided.

Within the Tipulinae some taxa, including *Eremotipula*, have cerci with a distinct lateral ridge, the ventrolateral surface vertical, not sloping, and the dorsal surface broad and flat. In cross section, this combination of features gives a three side appearance. The derived condition is difficult to determine. The alternative condition (state 0) is found in *Platytipula*, *Nephrotoma*, basal tipuline and the limoniine genera examined, and is here considered plesiomorphic.

49. *Female: Infra-anal plate: setae.*

0 = Setae of infra-anal plate undifferentiated.

1 = Setae of infra-anal plate differentiated: long setae along apical border, very short, dark setae more proximally.

The infra-anal plate or lobe is located below the cerci, and is generally considered the eleventh sternum (Tjeder 1958, as subanale; Frommer 1963: 584). In the *Vestiplex-Lunatipula* group, the lobe can have long setae, mostly apical, as seen in *Platytipula* and outgroup genera, or long and short setae, as seen in *Eremotipula* and most species of *Lunatipula*, *Triplicitipula* and *Setitipula*. The latter state is considered derived.

50. *Female: Eighth sternum: flatness.*

0 = 8S and hypogynial valves enclosing genital chamber.

1 = 8S broad and flat, not enclosing genital chamber.

In most Tipulinae, the eighth sternum is developed laterally and wraps up and around the genital chamber. In a few groups, such as the genus *Megistocera*, and subgenera *Vestiplex*, *Odonatisca* and *Serratipula*, the female eighth sternum is flattened and not so developed laterally.

51. *Female: Valvulae: apex.*

0 = Apex of fused valvulae a simple point.

1 = Apex of fused valvulae trifid.

The fused valvulae lie beneath the ninth tergum and are generally thought to be the remnants of the ninth sternum (Tangelder 1985, Byers, 1961). As noted by Tangelder (1985) for the Tipulinae, the "shape and size of the fused valvulae

vary among the different taxa and they may provide phylogenetically important characters." Within the Tipulinae, the median portion is generally developed into a long slender blade strongly narrowed to the simple apex, considered here plesiomorphic within the Tipulinae. In *Vestiplex* and *Odonatisca*, the apex of the fused valvulae is uniquely trifid.

52. *Female: Valvulae: venter.*

0 = Valvulae with smooth surface ventrally.

1 = Valvulae with dissected margin ventrally.

Although lightly sclerotized and smoothly margined in most Tipulinae, the ventral edge of the valvulae is finely dissected in three species of *Lunatipula* examined, *flavocauda* and *tergata* (*tergata* group), and *unicincta* (*unicincta* group)

Several additional characters might be useful in future studies, particularly as the distributions of the states are more clearly determined. I briefly list them below.

A. *Male: acrotergite of ninth tergum.*

Some taxa have a complete border, others have the border narrowly or widely interrupted medially.

B. *Male: sclerotized plates on the proctiger.*

Although this is obviously an overall reduction feature (more extensive sclerotization in the more basal taxa of Tipulinae), with most taxa lacking the sclerites entirely, there is certainly some intriguing variation among those species which possess the sclerites.

C. *Male: beak of inner dististyle with carinae or ridges.*

This feature can vary extensively within a subgenus (e.g., *Eremotipula*).

D. *Male: connection between the ventral plate of the ninth tergum and sp2.*

Weak to strong anterior connections are seen between the plate and sp2, with stronger connections developed among some of the subgenera.

E. *Male: dark setae on inner dististyle.*

The number and distribution of subequal short, dark setae on the lateral surface of the inner dististyle are quite variable. The presence of these setae is probably symplesiomorphic at the level of the ingroup. The analysis of species relationships

for *Eremotipula* makes use of the distribution of these setae (see character 34).

F. Male: vesica.

Some variability is seen in the overall structure, particularly the lateral arms.

Parsimony Analyses

Outgroup Analysis 1. The large size of the data matrix (Table 3) prevented exact search algorithms from being used in either analysis. Characters were treated as additive (ordered), and analyzed through a heuristic search algorithm in PAUP with the following parameters: ADDITION = simple, HOLD = 10 trees at each step, BRANCH SWAP = Tree-bisection-reconnection (7,129,321 rearrangements tried), MULPARS, and zero length branches collapsed. The analysis resulted in 1016 trees of length = 159 (filtered to 787 trees), consistency index (CI) = 0.352 and retention index (RI) = 0.623. Successive approximations character weighting (SACW) after two heuristic searches

yielded six trees, CI = 0.562, RI = 0.805. The strict consensus tree (Fig. 12) shows conflict only in the positions among *Labiotipula*, a clade containing *Hesperotipula streptocera* and *Triplicitipula*, and *Lunatipula* s. str. + *Eremotipula*, and lack of resolution within a clade containing some species of *Lunatipula* and the subgenus *Eremotipula*. The subgenus *Eremotipula* is monophyletic, within a clade of *Lunatipula* species, including *lunata*.

Outgroup Analysis 2. Characters were treated as non-additive (unordered), and the parsimony analysis run as in analysis 1 above, with 306,623 rearrangements tried. The analysis resulted in 44 trees of length = 150, consistency index (CI) = 0.373, and retention index (RI) = 0.625. After two heuristic searches through SACW, nine trees were found, CI = 0.576, RI = 0.812. The strict consensus tree (Fig. 13) is well resolved, with conflict only within a clade containing *Eremotipula* and some *Lunatipula* species, and also with *Pterelachisus* and *Lunatipula dorsimacula*. The position and monophyly of *Eremotipula* is as in analysis 1.

Table 3. Character state matrix for the *Lunatipula-Vestiplex* subgeneric group of the genus *Tipula*. The subgenus *Platytipula* (the first listed taxon) was used as the outgroup.

Character number	5	10	15	20	25	30	35	40	45	50	
<i>Platytipula</i>	00000	????0	000??	??000	0?0??	00000	00???	00000	00000	00000	00
<i>Serratipula</i>	00001	01001	00100	00100	10100	00000	00???	01010	01100	01001	00
<i>Pterelachisus</i>	00001	00102	00100	00100	0?100	00000	00???	00001	01000	00000	00
<i>Vestiplex</i>	00000	????0	01100	00000	0?0??	00000	00???	01011	10100	01001	10
<i>Odonatisca</i>	00001	01100	00110	10110	10101	00000	00???	01011	10100	01001	10
<i>Lindnerina</i>	10001	01001	01110	10110	10100	10000	00???	10101	01100	00100	00
<i>Setitipula</i>	11001	01100	10110	00100	11100	10000	01000	10101	01100	00010	00
<i>Labiotipula</i>	11111	01100	12111	11110	11101	10001	01011	10101	01100	00100	00
<i>Hesperotipula streptocera</i>	01101	00103	?2111	11110	0?101	10001	01???	10000	00110	10?00	00
<i>Hesperotipula chlorion</i>	11001	01003	?2100	00111	111?1	10001	01?00	10011	01101	00100	00
<i>Triplicitipula</i>	11001	01102	12111	11110	0?101	10001	01111	10101	01?00	00110	00
<i>Eremotipula incisa</i>	11111	11102	12111	11111	11111	11101	01111	10101	01100	00110	00
<i>Eremotipula impudica</i>	11111	11102	12111	10111	11111	11101	01011	10101	01100	00110	00
<i>Lunatipula lunata</i>	11101	00102	02111	11111	11111	11211	11111	10101	01100	00010	00
<i>Lunatipula translucida</i>	11101	01112	12110	10111	11101	10211	11111	10101	01100	00100	00
<i>Lunatipula aspidoptera</i>	00001	01102	10110	10111	11110	11211	01111	10001	01100	00110	00
<i>Lunatipula flavocauda</i>	11101	01112	02100	10111	11111	11211	01100	10001	01100	00010	01
<i>Lunatipula atrasumma</i>	0000?	????1	01110	10100	110??	10200	00???	10001	10?10	10?10	00
<i>Lunatipula dorsimacula</i>	00001	00100	10100	00100	0?100	10001	00???	00011	01000	00000	00
<i>Lunatipula boregoensis</i>	00001	01103	?0111	11100	10101	10001	01000	10001	01101	00100	00
<i>Lunatipula bisetosa</i>	11101	01102	02100	00111	11111	10211	11111	10011	01100	00110	00
<i>Lunatipula duplex</i>	11101	01102	?2110	11110	11111	10011	01111	10101	01100	00000	00
<i>Lunatipula fascipennis</i>	11101	01002	02100	00111	11111	10011	01011	10001	00110	00000	00
<i>Lunatipula vernalis</i>	11101	01102	02110	00111	11101	10211	01011	10001	01110	00010	00
<i>Lunatipula uncinata</i>	11101	01102	02100	00111	11111	10211	11011	10101	01100	00110	01

Preferred Cladogram. The above cladograms, based on a very preliminary sampling of in- and outgroup taxa, grouped *Eremotipula* with *Lunatipula lunata*, embedded within a group of a number of *Lunatipula* species. Due to the huge number of species represented in the series of subgenera, this analysis can only hope to serve to point out those taxa useful as outgroups for a species level phylogenetic analysis of *Eremotipula*, and as an outline for future research within the *Lunatipula-Vestiplex* complex. Although the above resolutions are parsimonious in this data set analyzed with the above parameters, they do require unlikely reversals and parallelisms in several complex characters thought to be groundplan synapomorphies for a revised concept of *Lunatipula* s. str. Investigations into alternative character transformations with MacClade examined *Eremotipula* as a sister group to a grouping of *Lunatipula* (Figs. 14, 15), not embedded as resulted in the above analyses. This preferred grouping required one overall extra step (tree length = 151), three additional steps in characters 20, 27, and 49, and two less steps in characters 11 and 29 (compare figs. 15 and 16). In the less parsimonious, but preferred cladogram (Fig. 15), the adminicular base (29), is derived once for *Lunatipula* s. str. and not subsequently reversed in *Eremotipula*, and the lateral plates of the adminiculum (28) are not derived from state 2 (mostly free curved hooks; *Lunatipula* s. str.) to state 1 (closely appressed plates, *Eremotipula*); both 28-2 and 29 are likely synapomorphies of a redefined *Lunatipula* as discussed below. The additional steps are in characters already with homoplasy (49) or less complex features requiring loss (20) or parallelism (27); both the latter two characters may prove synapomorphies of the two subgenera combined. This preferred cladogram (Figs. 14, 15) serves as the point for discussion.

Discussion of Outgroup Relationships

As can be seen from the cladogram (Fig. 15), the sister group of *Eremotipula* is the species *Tipula incisa*. Until this study, *incisa* was considered to be in the subgenus *Lunatipula*. The monophyly of the subgenus *Eremotipula* + *incisa* is strongly supported, based on the ventral plate shelf (6) and the lateral plates of the adminiculum (28-1), both unique features with little or no subsequent reversals (see also discussion of monophyly for in-group analysis). In addition, the subtergal process

(4) can probably be considered a synapomorphy, although a process also occurs in *Labiutipula*. These two subgenera do not otherwise appear closely related, and I consider the similarity of the processes as probably convergent.

The sister group of *Eremotipula* + *incisa* (hereafter considered together as *Eremotipula*) is most certainly a portion of *Lunatipula*, including the type species, *lunata* (Fig. 15). This grouping of *Lunatipula* is called here *Lunatipula* s. str. *Eremotipula* and *Lunatipula* s. str. share several convincing synapomorphies, namely the presence of a crest on the inner dististyle (20) and a hair patch on the mesal surface of the outer basal lobe (24, reversed in only one species). In addition, the expansion of the median lobe of the adminiculum (27), shown here as a parallel development in the two groups, due to the reversals among some of the *Lunatipula* species examined here, may constitute a synapomorphy, once a more complete sampling of *Lunatipula* is undertaken. Certain of these characters have been reversed in some species in both groups.

Lunatipula, as presently classified (Theischinger & Theowald 1981), is certainly not a monophyletic group, based on the characters used in this analysis (Figs. 12-14). A core group, *Lunatipula* s. str., is a natural grouping based on several striking synapomorphies (Figs. 14-15). The basal plate (29) of the adminiculum is unique and unreversed in this resolution (although as noted above not in the most parsimonious cladogram). The curved, hook-like lateral plates (28) of the adminiculum, lacking only in *duplex* and *fascipeunis*, are also a convincing feature. Both characters are complex morphological features that are certainly worthy of special study for use in delimiting a monophyletic *Lunatipula* s. str. The produced corners of the eighth sternum (31) and development of a genital bridge (11-0) may also be synapomorphies at this level, but would require subsequent reversals in some species. Based on the small number of species examined here, one third to over half the species currently placed in *Lunatipula* may remain in a more restricted *Lunatipula* s. str.

The remainder of the studied species of *Lunatipula* s. lat. are scattered throughout the cladogram (Fig. 14), confirming the suspicion that this subgenus at present is an artificial group consisting of an assortment of primitive to highly derived species. The four species excluded from *Lu-*

natipula s. str. occurred in as many locations along the cladogram, from rather basal (*dorsimacula*) to highly derived (*incisa*). When extrapolated to the 450+ species now placed in the subgenus, the polyphyly of *Lunatipula* s. lat. takes on major importance for any analyses of relationships subsequently undertaken in this section of *Tipula*. Since only a few species of *Lunatipula* were examined in this study, I will say little here concerning the detailed relationships of these species.

Although *Eremotipula* and *Lunatipula* s. str. appear to form sister groups, the close relatives of these two subgenera combined are not known (Fig. 14). *Triplicitipula* is placed in a more derived position than *Labiotipula*, based on the complete closure of the male basistyle (10), presence of paired medial groupings of setae on the apex of the male eighth sternum (33), and development of differentiated setae on the female infra-anal plate (49). State 2 of character 10 is seen elsewhere only in the functional outgroup *Pterelachisus*, and I believe it is probably informative for grouping *Triplicitipula*, *Lunatipula* s. str. and *Eremotipula*. Conversely, the frequency with which the inner margin of the basistyle has been reduced throughout the genus *Tipula* should imply caution in placing much weight on this character alone. The medial setae of the eighth sternum (33) have been reduced or modified within *Eremotipula*. Differentiated infra-anal plate setae are seen elsewhere in *Setitipula*, and are lost in some species of *Lunatipula*.

Several characters support a close relationship of *Labiotipula* with *Eremotipula*, *Lunatipula* s. str. and *Triplicitipula* (Fig. 14). Most convincing is the development of differentiated, isolated and thickened setae laterally on the apex of the eighth sternum (34, 35), as 34 is reversed subsequently in only one species, *flavocanda* (in which all setae in this area are reduced); thickened setae are lost in some *Lunatipula* s. str., and *Eremotipula*. Less support is offered by the presence of a median convexity of the female eighth tergum (38) as this is found outside the grouping, and is extensively lost within *Lunatipula* s. str. This grouping of three subgenera, *Labiotipula*, *Triplicitipula* and *Lunatipula* s. str., with *Eremotipula*, formed the outgroups for the analysis of species relationships for *Eremotipula* (see following ingroup analysis).

The male and female genitalia of *Hesperotipula* (based on the type species *streptocera*) are highly apomorphic, and this has presented problems in

determining homology. *Hesperotipula* may be related most closely to either *Labiotipula* or *Triplicitipula*. The characters of the male eighth sternum (33–35) which would shed light on this are impossible to code for *Hesperotipula* as the apex of the eighth sternum is highly modified in the type species and many other members of the group. Interestingly, the two species in the analysis placed presently in *Hesperotipula*, *streptocera* and *chlorion*, are not supported as monophyletic.

All of the above five subgenera form a monophyletic group based on the synapomorphy of dorsomedian lobes on the male ninth tergum (3). The inclusion of the (*Lu.*) *boregoensis* species group and *Hesperotipula chlorion* group with these five subgenera as a natural group is strongly supported by numerous characters of the male genitalia, including features of the A9S (15, 16, 17, for *boregoensis* only), an eighth sternum which is widest basally (30) a smooth, not pilose, outer basal lobe (25) and striae on the dorsum of the upper beak of the inner dististyle (19). This latter feature is seen elsewhere in *Odonatisca* and *Lindnerina*. *Lunatipula boregoensis* and *Hesperotipula chlorion*, although not supported as sister species, share the unique feature of a protuberance on the female tenth tergum (45).

The subgenus *Setitipula* is the sister group of the above taxa, as it shares with the above subgenera the derived features of differentiated setae of the ninth tergum (2) and long setae of the apex of the eighth sternum (32); the latter character is unique and unreversed. In addition, the grouped basiconic pegs (22) may be a synapomorphy here, as the pegs in the (*Lu.*) *atrasumma* group are possibly not "grouped" (they occur in a single short row). Along this branch, sp1 becomes shortened and isolated from the basistyle (11), a feature later reversed in *Lunatipula* s. str.

Lindnerina and the (*Lu.*) *atrasumma* group, are grouped here at the next basal node, but the median furrow of the ninth tergum (1) possibly indicates that *Lindnerina* is more derived. Synapomorphies uniting these two groups with the derived subgenera are the dorsal spine of the adminiculum (26) and a lengthened and usually slender intromittent organ (36). The female of *Lunatipula atrasumma* has highly modified genitalia, as shown in the numerous parallel or reversed characters (41, 42, 44, 46, 49). *Lindnerina*, based on many other features, is not closely related to *Labiotipula* and *Eremotipula*, and the median process

(4) differs in details, so homology between the process of *Lindnerina* and that of the other two subgenera is not supported. The processes of the other two groups are similar and may be homologous; however, other characters suggest that they are not sister groups, and that the resemblance is a parallelism. This awaits testing when other taxa related to these subgenera are examined. The process is here considered a synapomorphy for *Eremotipula* (see discussion of phylogenetic analysis of *Eremotipula*).

The grouping of *Serratipula*, *Odonatisca* and *Vestiplex*, and the further sister grouping of *Vestiplex* and *Odonatisca* is surprising, and based entirely on developments of the female genitalia. These include an emarginate 8S (37), roughened or toothed cerci (47) flat 8S (50) and tripartite valvulae (51), all unique and unreversed in this analysis. This support must be looked at with some caution, as no male characters support these groupings, and the toothed, shovel-like cerci and strap-like ninth tergum have been postulated as adaptations for deep boring oviposition, known to occur in *Odonatisca* and *Vestiplex* (Hemingsen, 1956). Nothing is known of oviposition in *Serratipula*, although the species are "range crane flies" in areas that undergo considerable summer drought (Alexander 1967). A similar combination of convergent features is seen in females of the *Eremotipula eurystyla* group and *Eremotipula lyrifera*, particularly the cerci development, flat 8S and short hypogynial valves. *Serratipula*, *Odonatisca* and *Vestiplex* share a unique, unreversed female character with the rest of the groups discussed so far, a short median point on the tenth tergum (43), indicating they belong somewhere at this level.

Based on male features, *Odonatisca* is a highly apomorphic group, with several features difficult to homologize with structures in the other taxa in this study. Although the appendages of the male ninth sternum are free distally (14), they are not pendulous as seen in other groups. Likewise the setae on these lobes are differentiated, but not typically shortened (16). *Vestiplex* has a highly modified male ninth tergum, and the lack of a ventral plate in this subgenus (relating to characters 5, 7, and 8) may not be the result of a primitive absence, but instead a derived reduction. In addition, the sclerotized pointed apices of the dorsal spiracular lobes of the larva, not seen outside this group of subgenera in the Tipuloidea (and not in *Pterelachisus* (Gelhaus 1986) or *Lunatipula dorsimacula* (Gelhaus, unpubl. data) is strong support for considering *Vestiplex* as part of the ingroup. Conversely, *Vestiplex* lacks several characters of the male inner dististyle (18, 23).

The subgenus *Pterelachisus* and species (*Lunatipula*) *dorsimacula* are basal in position, lacking the thickened band on the ventral plate of the ninth tergum (7), basiconic pegs (21) and having a long point to the female 10T (43). Both do have a number of male characters relating them to the other ingroup taxa, including a ventral plate (5) with an anterior process (8), development of a separate A9S (13, unique and unreversed), inner dististyle shelf (18, in all taxa except *Vestiplex*), and presence of outer basal lobe (23, also lacking in *Vestiplex*). Female characters are the partial fusion of the ninth and tenth terga (40) and bare tenth tergum (42). The ventral plate has not been noted in previous works and its presence, along with the other characters, may form a good synapomorphy demonstrating the monophyly of all the in-groups in the analysis.

Comparisons to Other Studies

No previous studies have treated the relationships of *Eremotipula*, although several researchers have treated in a limited way the relationships among the *Vestiplex-Lunatipula* group of subgenera. Although it is interesting to contrast these schemes with the cladogram derived in this present work, one must keep in mind that these earlier researchers were using a different classification (e.g., *Lunatipula* may include *Labiotipula*, *Eremotipula*, etc.) and examined a different set of species than I have; therefore, results are not entirely comparable. In particular, in artificial groupings such as *Lunatipula*, the choice of which species to study becomes critical to the final results.

Comparisons to Other Studies

Theowald (1958) considered *Vestiplex* and *Lunatipula* (*lunata* group) to be closely related, based on an increasing sclerotization of the dorsal spiracular lobes of the larvae. According to the cladogram presented here, *Vestiplex* and *Lunatipula* s. str. (also based on *lunata*) are only distantly related, with *Lunatipula* s. str. highly derived and *Vestiplex* in a very basal position. It is possible that the single larval character on which Theowald based the relationship might be convergent but more likely the tendency for development of sclerotized, hook-like lobes is part of the groundplan for the entire *Lunatipula-Vestiplex* group.

Frommer (1963) considered *Vestiplex* close to *Yamatotipula* based on a fusion of the ninth tergum and sternum and a membranization of the midline of the ninth sternum. This latter feature is certainly plesiomorphic (see Tangelder 1985), as it occurs in most Tipulinae. The fusion of the ninth segment is found also in at least *Platytipula* and may be convergent or symplesiomorphic.

Theowald (1958) and Savchenko (1966) considered the (*Lu.*) *livida* and *falcata* groups and *Odonatisca* (= *juncea* species group of Theowald) as closely related, and certainly they appear to form a monophyletic group based on characters of the larval spiracular lobes, pupal thorns and male and female genitalia. Both authors ally these groups with *Vestiplex* and *Lunatipula* (*lunata* group), but this is not supported by my analysis, at least in regards to the *Lunatipula lunata* group. The species now placed in *Odonatisca* probably have more apomorphic characters than those in the *livida* and *falcata* groups of *Lunatipula*.

It is difficult to reconcile the classification of *Lunatipula* s. lat. provided by Theowald & Oosterbroek (1990), which only includes Palearctic species groups in the Middle East, and the cladogram of relationships presented in this study, which includes Palearctic and Nearctic groups and species. The cladogram of Theowald & Oosterbroek (1990) adapted the groupings of Riedel (1913), suggesting these groupings are overlaid in part by synapomorphies. Unfortunately, it is based on only six male genitalic characters (none illustrated or described in depth) with no discussion of homoplasy. In addition, no synapomorphies are given for their concept of *Lunatipula*. Several of their characters do agree with those in the above analysis, such as thickened setae of the eighth sternum, while others appear unique to the Palearctic fauna, or were possibly used without being aware of subsequent modification and reversal.

Summary

In summary, the preliminary hypothesis of relationships allows several points to be made: 1. *Eremotipula* appears monophyletic, and includes *Tipula incisa*. 2. *Lunatipula*, as presently constituted, is a polyphyletic grouping, with a mixture of relatively plesiomorphic to highly derived species. Based on extrapolation from the species examined in this study, and knowledge of the

species groups, fully one-third or more of the species show close relationships to other subgenera, including *Pterelachisus*, *Triplicitipula* and *Odonatisca*. 3. A subset of *Lunatipula* (here called *Lunatipula* s. str.) based on the type species *T. lunata*, is supported by several synapomorphies of the male genitalia, most importantly the adminiculum with a broad expanded base (29) and with hook-like lateral plates (28). This grouping is the sister group of *Eremotipula*, based on the possession of a hair tuft (24) and crest (20) on the inner dististyle. 4. The monophyly of the *Lunatipula-Vestiplex* series of subgenera is preliminarily supported by numerous characters of the male and female terminalia.

Future Study

The preliminary nature of the conclusions presented here cannot be overstressed. Many more taxa need to be examined before we can hope for a clear understanding of the relationships of this entire clade. Most characters used in this analysis have not been previously considered as useful for indicating relationship, and several have not even been mentioned in descriptions, for example, the differentiated setae on the ninth tergum (character 2), ventral plate of the ninth tergum (character 5) and shape of the eighth sternum (character 24). By contrast, many of the characters often used in relating species of *Tipula* were not found to be useful at this level of analysis, e.g., the shape of the dististyles or of the lobes of the ninth tergum, and are probably best used at the species-group level, as realized for *Eremotipula* (see following analysis). The reliability of the characters introduced in this study cannot be tested by examining previous species descriptions as no mention will be found of them there. Instead, only a careful examination of actual specimens will illuminate the relationships among these subgenera.

ANALYSIS OF SPECIES RELATIONSHIPS IN *Eremotipula*

The analysis of the phylogenetic relationships among the species of *Eremotipula* was based on 59 mostly male and female genitalic characters (Table 4) distributed among mainly 15 separate parts or body areas, with those of the male adminiculum contributing the most to the analysis. The analysis presented here builds upon that in

Gelhaus (1989) but adds female genitalic and other characters and numerous additional taxa.

Outgroups relevant to understanding the phylogeny of *Tipula* (*Eremotipula*) were determined from the outgroup analysis, presented in the previous section. These taxa include the distantly related *Tipula* (*Platytipula*) (used also as outgroup for subgeneric analysis), and the clade formed of the closest relatives of *Eremotipula* taken from the strict consensus tree of the outgroup analysis: the subgenera *Tipula* (*Labiotipula*), *T.* (*Triplicitipula*) and *T.* (*Lunatipula*) s. str. (4 species including the type species *lunata*, *bisetosa*, *duplex*, and *translucida*). These groups were all included in the parsimony analysis to allow simultaneous parsimonious resolution of in- and outgroups relationships (Nixon & Carpenter 1993, Swofford & Begle 1993). Several characters that are invariant for the species of *Eremotipula* were included in the analysis to allow resolution of included outgroups; these are characters 25, 31, 41, 51, and 58.

Character Analysis

1. Wing patterning along vein CuA and m-cu.

0 = wing membrane along vein CuA and crossvein m-cu concolorous with surrounding coloration.

1 = wing with broad, light brown band along vein CuA and crossvein m-cu, contrasting with surrounding coloration.

There is much variability in the wing patterning among the outgroup taxa and in *Eremotipula*. Commonly, though, the wing is uniformly light brown with some whitening along the cord (stigma to discal cell) in the outgroups. Within *Eremotipula*, *incisa* is one of the most variably and distinctly patterned species. Brown spots at the origin of Rs and the end of Sc, light brown streaking in several cells and yellowing of cells *c* and *sc* can be found scattered among the species of the subgenus.

The patterning described in state 1 above is found in the *kirkwoodi* species subgroup and in *sinistra* and *middlekauffi* within *Eremotipula*. I am not aware that it occurs in any of the outgroups and consider it a derived condition.

2. Wing patterning—cell r_5 .

0 = wing mostly unicolorous, or if contrastingly patterned with brown and white, then r_5 not

white, or white coloration in r_5 not continuous with that in cell *r*.

1 = white color in cell r_5 continuous with that in cell *r*, reaching arculus.

This pattern of the wing is unique to the species in *kirkwoodi* subgroup within *Eremotipula*, but sporadically occurs in the entire genus *Tipula*, e.g., the *tricolor* species group of the subgenus *Yamatotipula*.

3. Leg coloration.

0 = legs yellowish brown, usually with contrasting brown femoral ring.

1 = legs dark brown, often with yellow ring preceding the area of the femoral ring.

The dark brown leg coloration is restricted to *sinistra* and *middlekauffi* among the species of *Eremotipula*, although some individuals of *sinistra* are not so distinctively marked. The legs of *melanderiana* and *helferi* are dark yellowish brown, but without the yellowish ring.

4. Setae of abdominal tergum 1.

0 = setae along posterior margin of tergum 1 not much longer than tergal setae immediately preceding them, all setae on tergum 1 dark.

1 = about 10 light brown setae along posterior margin of tergum 1, each 4–5 times as long as dark setae elsewhere on tergum 1 (Fig. 343).

Elongate setae as in state 1 above are found only in *Triplicitipula* among the included outgroup taxa.

5. Male eighth sternum: apical membranous margin.

0 = apical membranous border nearly straight, without a broad medial lobe (Fig. 240).

1 = apex with a broad, short, flattened, medial lobe (Fig. 182).

2 = as in 1, but lobe elongate (Fig. 201).

State 0 occurs in all the outgroups examined, as well as in most species of *Eremotipula*.

6. Male eighth sternum: apical setae.

0 = setae along apical margin in two groups of medial and lateral setae, the medial setae much shorter than lateral ones (Fig. 67).

1 = all setae of nearly equal length and organized into a broad band, band narrowly divided at midlength (Fig. 81) or band continuous (Fig. 241).

Labiotipula has a divided setal band. Short medial setae, organized into two groups, are found in

most of the species of *Lunatipula* s. s. and *Triplicitipula* examined, as well as two species of *Eremotipula*, *incisa* and *melanderiana*, and is here considered as the plesiomorphic condition within *Eremotipula*. See also character 33 in the outgroup analysis.

7. Male eighth sternum: lateral sclerites.

0 = setal band with a sclerite on either end (Figs. 241, 330).

1 = setal band without lateral sclerites (Fig. 422).

All the species of *Triplicitipula* and *Lunatipula* s. s. I examined possessed large, usually articulated sclerites with several setae. None of the species examined in the out-groups lacked the sclerite entirely. Both *incisa* and *melanderiana* have well-developed sclerites similar to those found in the outgroup taxa, with the remaining species of *Eremotipula* showing a reduction or absence of the sclerites, considered apomorphic. See also character 34 in the outgroup analysis.

In some species, the lateral sclerites extend inward, meeting medially in *incisa*, *melanderiana* and *larreae* (Fig. 81), but not meeting in some other species, such as *dissepina* (Fig. 375).

8. Male eighth sternum: sclerites near membranous lobe.

0 = lateral sclerites present or absent, but no isolated sclerites at or near base of membranous lobe.

1 = lateral sclerites absent in "typical" position (see character 7), but isolated sclerites at or near base of lobe (Figs. 403, 423).

State 1 is found only in *lyrifera* and *sackeni*, two species in the *diversa* species group. Whether these sclerites are homologous to the "lateral" sclerites (character 7) is not known, as the sclerites on the membranous lobe are in a different position. The position of the sclerites also differs between the two species, those of *sackeni* extending onto the lobe, those of *lyrifera* being only near the base of the lobe or sometimes absent.

9. Male eighth sternum: lateral setae.

0 = one or more thickened, elongate setae (longer than medial setae) on lateral sclerite, the setae usually convergent mesad (Figs. 44, 67, 81, 113).

1 = All setae of nearly equal length and thickness, none convergent (Figs. 225, 265).

Thickened lateral setae in some form are seen in nearly all species examined in *Lunatipula* s. str. (*bisetosa*, *duplex*, *lunata*, *translucida* and others), *Triplicitipula* and *Labiotipula* (see also character 35 in the outgroup analysis). Within *Eremotipula*, a progression in reduction can be seen when comparing the number of setae, their lengths, thickness and coloration.

10. Male eighth sternum: setal group.

0 = setae of band extended toward membranous lobe along midline, but no groups of setae short or isolated from remaining setae in band (Fig. 391).

1 = setae of band extended toward membranous lobe along midline, shorter and isolated from remaining setae in band (Fig. 422).

State 1 is found in *diuidiata*, *diversa* and *sackeni*, with the same setae shorter but not isolated from the band in *lyrifera*.

11. Male eighth sternum: membranous lobe.

0 = membranous intersegmental area between eighth and ninth sterna flat, without membranous lobe.

1 = membranous lobe minute to small, usually conical or pimple shaped, concealed between eighth and ninth sterna (Figs. 241, 242).

2 = membranous lobe larger, of a broad and linguiform shape, visible among 8S setal band (Figs. 82, 330).

3 = membranous lobe elongate, digitiform, and visible among 8S setal band (Figs. 306, 199).

A membranous lobe between the eighth and ninth sterna is found in most species of *Eremotipula*, absent in only *incisa* and *melanderiana*. I see no homologous structure in the outgroups. Although *Tipula* (*Lunatipula*) *rabiosa* and *T. (L.) aspidoptera* both have a large, quadrate membranous lobe along the edge of the eighth sternum, these lobes are not in the same position, and the structure of the lobe and microtrichia differs from that found in species of *Eremotipula*.

Although the lobes are always in the same position among the species of *Eremotipula*, lobe morphology varies greatly among the species. The lobe is small and hidden in some species (state 1), some have broad lobes that differ in length and shape of the apex (state 2), while others have narrow, elongate lobes, either flattened or cylindrical (state 3). Microtrichia may be present or absent on either broad or narrow lobes (see character 12).

12. *Male eighth sternum: lobe surface.*

0 = membranous lobe with microtrichia, or at least tuberculate.

1 = membranous lobe glabrous, at most transversely wrinkled (Fig. 391).

Most species of *Eremotipula* have lobes with microtrichia, or in the *kaibabensis* species group, a gradation between microtrichia and a tuberculate condition. In the outgroup taxa examined, a lobe is absent (see preceding character) but membrane with microtrichia is found in the same area between the eighth and ninth sterna. A glabrous, nearly smooth membranous lobe (state 1) occurs in the *diversa* species group only.

13. *Male ninth tergum: development of dorsal lobes.*

0 = dorsal lobes scarcely or not produced (Fig. 120).

1 = dorsal lobes broad, short with acute to subacute apices (Figs. 49, 60, 86, 339).

2 = lobes extended, broad to narrow, apices usually acute (Figs. 160, 234, 378).

Dorsal lobes are found among species of *Lunatipula* s.s and *Labiotipula*, with their shapes varying tremendously even among the few species examined. Lobes are lacking in *Triplictipula* species examined (see also character 3 of outgroup analysis). Within *Eremotipula*, the dorsal lobes vary from absent (*helferi*), slightly present with medial margin more extensive than lateral one (e.g., *incisa*) to well developed, with medial and lateral margins of lobe often nearly equal in length (e.g., *macracantha*).

14. *Male ninth tergum: shape of dorsal lobes.*

0 = dorsal lobes not subparallel, margins not smooth.

1 = dorsal lobes subparallel, usually with smooth margins (Figs. 378, 383).

The dorsal lobes of the *diversa* group, excluding *disspina*, are unique in *Eremotipula* in having parallel, medial margins. The lobes in *lyrifera* appear additionally modified (Fig. 395), with the homology of lobes to the rest of the species in the *diversa* group being clear, particularly when comparing the border of the swollen area in *lyrifera* to the lobe border in the other species.

15. *Male ninth tergum: subtergal process.*

0 = subtergal process not present (posteromedial margin of the ventral plate flat and undeveloped).

1 = subtergal process present, but only as a minute point arising from posteromedial margin of ventral plate (Fig. 121).

2 = subtergal process short, somewhat depressed (at least basally), apex rounded and smooth, length one-third that of tergum (Fig. 49).

3 = subtergal process short, somewhat compressed and rod-like (at least basally), apex subacute and smooth, length usually one-third that of tergum (Fig. 160).

4 = subtergal process elongate, somewhat laterally compressed, apex acute, pale, margin irregular (often ridged or lacinate), length more than one-half that of tergum (Fig. 2).

A subtergal process, at least the lacinate structure in many species, may be unique to *Eremotipula*, with no comparable structure seen in the outgroups (see outgroup analysis). Although median projections are seen in *Labiotipula*, *Triplictipula* and some species of *Lunatipula*, these all appear to have developed differently from the ventral plate. Conservatively, *Labiotipula* has been coded as state 3.

16. *Male ninth tergum: microtrichia of subtergal process.*

0 = subtergal process with microtrichia.

1 = subtergal process without microtrichia.

Subtergal processes do not occur in the outgroups (except possibly *Labiotipula*), making them uninformative for this character.

17. *Male ninth tergum: ventral plate shelf and lobe.*

0 = ventral plate without curled shelf along anterolateral edge.

1 = ventral plate with curled shelf with scarcely distinct, flat lobe (Fig. 54).

2 = as in state 1, but lobe of medium length, apical margin rounded (Fig. 264).

3 = as in state 1 but lobe elongate, narrow.

4 = as in state 3 but lobe broad (*kirkwoodi*).

5 = as in state 2 but ventral lobe margin irregular

6 = as in state 2 but lobe very broad, flat with rounded apical margin

7 = as in state 2 but lobe thick (extending from flat base) with truncate to nearly truncate apex.

The presence of a ventral plate shelf and lobe is unique to *Eremotipula* based on my examination of specimens for the outgroup analysis and published descriptions and illustrations. Nothing comparable is seen in any of the outgroup taxa,

with at most small projections extending from the ventral plate in *Tipula* (*Lunatipula*) *lunata*.

Within *Eremotipula*, *helpferi* lacks the shelf and lobe, with only a narrow posterior flange on the plate, possibly representing the remnants of the shelf. Among the other species, the lobe takes a variety of shapes, from scarcely evident (e.g., *biproducta*) to elongate, flat (e.g., *diversa* group) to thick (e.g., *sinistra* group), as noted in the coding.

18. Male ninth tergum: line on ventral lobe.

0 = ventral lobe of ninth tergum without transverse subapical line.

1 = ventral lobe with transverse, subapical line (Fig. 429).

This character is found in *sackeni* and *diversa* in the *diversa* group.

19. Male ninth sternum: membranous protuberance.

0 = membranous, midventral region of ninth sternum without distinct protuberance, although entire area from adminiculum to acrosternite may be slightly swollen.

1 = midventral region with membranous protuberance with elongate microtrichia located only just anterior to A9S (Fig. 68).

2 = region with membranous protuberances as in 1, and rounded protuberance just posterior to acrosternite (Figs. 92, 93).

3 = region only with rounded protuberance just posterior to acrosternite (Fig. 149).

The protuberance was not seen in the outgroup species examined, but a differently-constructed, mostly membranous structure is seen in other species (e.g., some *Lunatipula* *unicincta* group species have well developed lobes, while in *bisetosa* this area is merely swollen). Within *Eremotipula*, I note that the area in *spinirecta* is distinctly swollen but not as a developed lobe.

20. Male appendage of ninth sternum: ventral lobe.

0 = ventral lobe of A9S fully sclerotized, not swollen proximally, and completely covered with setae (Fig. 44).

1 = ventral lobe of A9S membranous distally, with setae only proximally (Fig. 62), lobe usually swollen proximally and abruptly narrowing in membranous region to apex.

Character state 1 is found only within *Eremotipula* and occurs in all of the species except for *incisa*. The membranous area is reduced in a few species, e.g., *biproducta* (Fig. 310). The ventral lobe

of the A9S in *incisa* is circular, entirely sclerotized, and covered completely by long, twisted setae, much as in the subgenera *Triplicitipula* and *Lunatipula* (*lunata*). The condition of this lobe varies considerably elsewhere within *Lunatipula*, but is never as described in state 1 (see also characters 13–16 of outgroup analysis). The species *anasazi*, *biproducta*, *pellucida* and *woodi* do not have the lobe swollen proximally, but have a membranous distal area. When the ventral lobe is circular (cf. *incisa*, *eurystyla*, subgenus *Triplicitipula*, Figs. 44, 92) it is hard to evaluate whether the lobe is swollen or not.

21. Male appendage of ninth sternum: ventral lobe setae.

0 = ventral lobe of A9S with setae twisted distally (Fig. 44).

1 = setae on lobe straight, equal in length to or exceeding those on the dorsal (proximal) lobe (Fig. 62).

2 = some or all setae on ventral lobe shorter (Fig. 162) and thicker than those on dorsal lobe, some markedly so, these setae directed laterally as a group (Figs. 77, 162, 342).

3 = some setae on ventral lobe thickened, although may be pale, other setae not thickened, and of similar length and thickness to those on dorsal lobe.

Completely straight setae are seen in all species of *Eremotipula* except *incisa*, and also in some species of *Lunatipula* s. str. (e.g., *rabiosa*, *translucida*). The presence of twisted setae, long and not noticeably thickened is seen in *incisa*, *Triplicitipula* and all other outgroups (see also character 17 in outgroup analysis).

In nearly all species of *Eremotipula*, the majority of the setae on the ventral lobe are thick and yellowish or reddish brown. Both *mitrata* and *schusteri* have greatly thickened setae (Figs. 137, 282), although their thickness, number and color differ between the two species.

In addition, these setae are also directed laterally, with the representation among taxa following closely with state 2. Laterally directed A9S setae appear to be unique to *Eremotipula* but not necessarily independent of state 2 and so isn't treated as a separate character here (but see Gelhaus 1989). This feature is not applicable to *mitrata* due to the few, greatly thickened setae (Fig. 282) and is incompletely expressed in *utahicola* (Fig. 107). The state of this character cannot be deter-

mined in *biproducta* as the setae are broken from the unique specimen (Fig. 310). The setae project in several directions in *spinosa*, although they are thickened and short (Fig. 318).

State 3 is seen in the *diversa* group, with *lyrifera*, *leiocantha* and *evalynae* all showing modifications of the ventral lobe setae. The other species in the species group as well as most species outside the group have darker, thickened short setae as noted.

22. Male appendage of ninth sternum: size.

0 = ventral lobe of A9S not large and protruded.

1 = ventral lobe of A9S large and protruded (Figs. 216, 225).

The ventral lobes of *byersi* and *impudica* are both large, but differ in overall shape from each other.

23. Male basistyle: dorsomedian projection.

0 = dorsomedian border of basistyle usually slightly curved, without a slight projection opposite arm of sp1 (Fig. 226).

1 = basistyle with triangular projection opposite arm of sp1 (Fig. 302).

State 1, a triangular projection opposite sp1, is found in *kaibabensis* and *dimidiata*. This may only represent the most developed condition of a more widespread character in the subgenus, as the other two members of the species group, as well as *schusteri*, have smaller but similarly shaped projections, and a small point is scarcely indicated in *artemisiae*. The condition in *pellucida* may be a modification of this state, possibly due to the huge expansions of the adminiculum which lie next to the basistyle (Fig. 195).

24. Male basistyle: inner margin.

0 = small or no lobe along inner border near base of sp2 (sp2 may be swollen).

1 = large, rounded flat upright lobe along inner border near sp2 base.

State 1 is unique to the *kirkwoodi* group.

25. Male basistyle: socket.

0 = basistyle with dorsomedian surface mostly membranous, with inner margin of "basistylar socket" incomplete, sp2 present.

1 = dorsomedian surface of basistyle with isolated sclerite between sp2 and posterior border.

2 = dorsomedian surface of basistyle sclerotized, forming a complete ring or socket dorsally.

See outgroup analysis discussion (character 10). State 1 is not represented among the taxa in the ingroup analysis but is among the outgroup analysis.

26. Male basistyle: dorsolateral lobe.

0 = outer margin of basistyle nearly straight or with only a slightly developed convexity in lateral aspect opposite posterior condyle of inner dististyle.

1 = basistyle with moderately projecting convex margin opposite posterior condyle of inner dististyle.

2 = basistyle with moderately projecting convex margin curled inward with spur or separated small lobe.

3 = basistyle with moderately projecting convex margin with inwardly directed short spine.

4 = basistyle with moderately projecting convex margin with elongate, inwardly directed spine opposite posterior condyle of inner dististyle.

5 = basistyle with a greatly developed convex margin which is truncate in lateral view.

6 = basistyle with a moderate to greatly developed convex margin formed into flat, wide triangular projection, directed posteriorly, apex acute or nearly so.

7 = basistyle with a moderate to greatly developed convex margin formed into a flat, wide triangular projection near inner dististyle, apex acute and directed dorsally.

8 = basistyle as in *incisa*.

9 = basistyle as in *biproducta*.

The dorsolateral aspect of the basistyle presents a wide variety of shapes within *Eremotipula* and among its near relatives, causing problems in understanding homology and determining transformation series for these projections of the basistyle in *Eremotipula*. Based on the few species of *Lunatipula* s. str. examined, no projection or lobe is precisely comparable to that of *Eremotipula* as the projection may occur opposite the anterior condyle of the inner dististyle (*lunata*), between the condyles (*rabiosa*), or bordering the ventral basistylar suture in *translucida*. Some species, such as *aspidoptera*, have a straight margin. The mere placement of this produced area opposite the posterior condyle in *Eremotipula* may constitute a synapomorphy for the subgenus, but this requires further testing as more species of *Lunatipula* s. str. are examined.

The derived states of character 26 are delimited rather arbitrarily, although the development of a rounded to triangular lobe on the edge of the basistyle can be arranged in a gradual series when many species are examined. Autapomorphic states abound in *Eremotipula*, e.g., *pellucida* or *biproduca* (Figs. 309, 310).

A short spine is seen in *spaldingi*, *byersi*, and some specimens of *impudica* (state 3). According to Riggins & Pimentel (1987), a taxon with a variable character state should be coded as unknown or be treated as two separate taxa; instead in this final analysis I have coded *impudica* as having state 3.

27. Male basistyle: posterior edge.

0 = posterior edge of basistyle not expanded.

1 = posterior edge of basistyle expanded along inner border, with shallow depression.

Unique to the *helferi* and *kirkwoodi* subgroups of the *eurystyla* group.

28. Male outer dististyle.

0 = outer dististyle with no anterior extension, often club-shaped or a narrow rod, dorsal margin convex (Figs. 46, 91).

1 = dorsal margin of outer dististyle usually straight, with short to elongate anterior extension ("beak"), apex narrowly rounded and mostly directed anteriorly (Fig. 228).

The shape of the outer dististyle in *Lunatipula* s. str. varies from small, erect and narrow, to club-shaped. No species examined has an anterior extension ("beak"), although the dististyle may be produced posteriorly. The outer dististyle of *incisa* is a narrow rod as in some *Lunatipula* s. str. A few additional species of *Eremotipula* (*eurystyla*, *dis-spina*) have club-shaped outer dististyles. The majority of species of *Eremotipula* have a characteristic, anteriorly produced dististyle, with this anterior area variable in length. Although a trend in lengthening was noted, I found this hard to measure in any meaningful way, as ratios used were easily skewed by the variation in the width of the dististyle at the base within a species or the difficulty in making repeatable measurements of the base *in situ*.

29. Male inner dististyle: crest development.

0 = crest well-developed anteriorly and closely appressed to lateral surface of upper beak, dorsal margin convex (Fig. 64).

1 = as in 0, but not closely appressed to lateral surface, dorsal margin convex or sinuous or concave (Figs. 76, 227).

2 = crest reduced in size and developed only posteriorly as lobe, posterior apex rounded (Figs. 163, 283) or posterior apex angulate, lobe nearly triangular in lateral view (Fig. 431).

3 = crest as in *spinerecta*.

4 = crest absent.

A crest on the inner dististyle is found only in *Lunatipula* s. str. and *Eremotipula* within this clade of subgenera. The crest in species of *Lunatipula*, when present, is similar to state 0, such as (*Lunatipula*) *lunata*, but it can be totally absent as well (e.g., *translucida*). Within *Eremotipula*, state 0 is found only in *incisa* and *melanderiana*. The crest in some other species of *Eremotipula* is similarly well-developed, but the dorsal margin is not simply convex. The remaining species show a progressive reduction in the crest, including progressive membranization. A crest is absent in most species of the *eurystyla* group.

30. Male inner dististyle: lamella.

0 = inner dististyle without lamella along lateral side of anterior half.

1 = inner dististyle with lamella as in *utahicola* and *baumanni*.

Although lacking a crest, these species have a more sclerotized lamella anterior of the crest position. Nothing similar is seen among the outgroup taxa.

31. Male inner dististyle: pegs.

0 = basiconic pegs absent from inner dististyle.

1 = basiconic pegs present.

See discussion under outgroup analysis (characters 21, 22).

32. Male inner dististyle: direction of OBL.

0 = OBL directed dorsally (i.e., perpendicular to longitudinal axis of base of dististyle) (Fig. 45).

1 = OBL directed dorsoposteriorly (i.e., at obtuse angle to base of dististyle) (Figs. 76, 163).

2 = OBL directed posteriorly (i.e., parallel to longitudinal axis of base) (Figs. 4, 319).

Among the outgroup taxa examined, a dorsally directed OBL occurs in all but one (*translucida*) of the species of *Lunatipula* s. str. and in *Triplicitipula*; it also occurs in two species of *Eremotipula*, *incisa* and *spinerecta*. The dorsoposteriorly directed OBL is seen in *melanderiana*, *larvae*,

remaining *eurystyla* group species, and *macracantha*, as well as in (*Lu.*) *translucida*. A posteriorly-directed OBL is found in all the remaining species of *Eremotipula* and not among the outgroups.

The OBL in *helferi* is quite apomorphic, with no distinct directionality to the lobe (Fig. 122); it was coded as "?".

33. Male inner dististyle: rotation of OBL.

0 = dorsal margin of OBL not curled or rotated laterally from the longitudinal axis (Fig. 64).

1 = dorsal margin of OBL slightly to greatly curled or rotated laterally from the longitudinal axis, rotation up to 90° (in which the mesal surface becomes dorsal (Figs. 4, 191).

At best, the OBL is only slightly rotated laterally in the outgroups and *incisa*, but the wide variety of complex shapes of the OBL in the outgroups makes the homology uncertain. Both *larreae* and *melanderiana* lack rotation and this was considered plesiomorphic. The most extreme rotation occurs in the *diversa* species group (Figs. 4–6) and this is considered apomorphic.

34. Male inner dististyle: OBL setae and ridge.

0 = lateral surface of OBL with setae scattered over surface, or few in number.

1 = lateral surface of OBL with setae in loosely organized line extending from anterior part of ID, a distinct patch of setae located between OBL and ID posterior condyle.

2 = lateral surface of OBL with setae mostly or only located along ridge on lower aspect of OBL, a distinct patch of setae located between OBL and ID posterior condyle.

3 = lateral surface of OBL with setae mostly or only located along ridge located on the more "medial" aspect of OBL, no distinct patch of setae located nearer base.

4 = lateral surface of OBL with setae mostly or only located along ridge located on "upper" aspect of OBL, no distinct patch of setae located nearer base.

Setae located on the lateral surface of the ID are usually of similar length, coloration (usually dark) and arise from distinct bases. In the outgroups and some species of *Eremotipula* examined, the setae are scattered over the OBL or are few in number. In some species of *Eremotipula* the setae on the OBL have distinct placement patterns. In addition, the short dark setae are closely associated with the ridge in the *diversa* group and in *sinistra*.

35. Male inner dististyle: OBL shape 1.

0 = no bend beyond base of OBL, shape broad, rounded and short as in *spinirecta*.

1 = no bend beyond base of OBL, shape broad, rounded apex, elongate as in *incisa*.

2 = no bend beyond base of OBL, shape broad, extended, expanded subapically, apex blunt as in *kirkwoodi* group.

3 = no bend beyond base of OBL, shorter, apex truncate as in *utahicola* group.

4 = no bend beyond base of OBL, short, shape oblong or nearly so as in *macracantha*.

5 = bend beyond base of OBL, shape as in *kaibabensis* (oblong OBL).

6 = bend beyond base of OBL, shape as in *impudica* group (OBL boot-shaped).

7 = bend beyond base of OBL, shape as in *pellucida* group (narrowed apically).

8 = bend beyond base of OBL, shape as in *sinistra* group (apex extended and narrowed).

9 = bend beyond base of OBL, shape as in *diversa* group (entire OBL elongate, apex narrowed).

Considering the diversity of structure of the OBL within *Eremotipula*, the diversity among the species of *Lunatipula* s. str., the sister group of *Eremotipula*, is not unexpected. The OBL of (*Lu.*) *lunata* is roughly similar to that of *melanderiana* and *larreae*, but the quite different OBL in (*Lu.*) *translucida* is similar to that of *incisa*.

A morphocline exists from the shape seen in the *kaibabensis* group and *macracantha* to the *sinistra* and *diversa* groups but there are shapes seen in the *madina* group and *pellucida*, for example, which are hard to place within this morphocline. Certainly OBL is bent beyond the base in all these species. Distinct shapes are seen as well in the *kirkwoodi* and *utahicola* groups, which lack a bend in OBL.

36. Male Inner dististyle: OBL shape 2.

0 = OBL flat, not excavated on lateral surface.

1 = OBL excavated laterally (Fig. 303).

Most species of *Eremotipula* have a laterally excavated OBL.

37. Male Inner dististyle: posterior margin.

0 = posterior margin of ID (dorsal to posterior condyle) straight or weakly concave (Figs. 381, 387).

1 = posterior margin of ID strongly convex (Figs. 5, 431).

A convex margin occurs among some species of the *diversa* group and is considered derived.

The margin in *evalynae* is only narrowly convex, while that of *diversa* and *sackeni* is broadly convex.

38. Male Adminiculum: lateral plates.

0 = lateral plates present as curved hooks, and not closely attached to body of adminiculum except at base, or lateral areas undeveloped.

1 = lateral plates closely attached to body of adminiculum with only apices free (as "dorsal lobes"), each plate shelf-like (Figs. 251, 253).

2 = as in 1, but apices fused to stem of adminiculum, and lobes not distinguishable (Fig. 96)

This character is a synapomorphy of *Eremotipula* and is more fully explained with the characters used in the outgroup analysis (e.g., character 27). In *incisa*, the adminiculum has a set of three plates laterally, with the single plate condition in the other species of *Eremotipula* assumed to be a fusion of these plates. In some species, each plate does appear to be narrowly interrupted approximately one third length from the base (Fig. 78), and may represent an incompletely fused condition. The lobes in several species are fused completely. The lobes in *byersi* and *dissipina* are short spines, but not comparable to the curved hooks as in many *Lunatipula*.

39. Male adminiculum: apex of dorsal lobes.

0 = dorsal lobes rounded apically.

1 = dorsal lobes short, with apices generally truncate (Figs. 329, 347).

2 = apical margin with several small points or teeth.

3 = apical margin with single or bifurcate, moderately large spines.

Coded as "?" are *eurystyla*, *utahicola* and *bau-manni*, which don't have free dorsal lobes.

40. Male adminiculum: dorsal lobes striate.

0 = dorsal lobes without transverse striae.

1 = dorsal lobes with transverse striae (Figs. 390, 401).

Strong striae are found on the dorsal lobes only in the *diversa* species group (excluding *dissipina*) with weak striae present in *helferi* and *larreae*.

41. Male adminiculum: median lobe.

0 = median lobe not developed or usually small and fully sclerotized.

1 = median lobe expanded and mostly pale, with dark sclerotization along border.

See outgroup discussion (character 27).

42. Male adminiculum: bifurcate beak of median lobe.

0 = median lobe with single beak, or margin rounded (Figs. 270, 400).

1 = median lobe with large spine, in addition to the distinct acute beak (Fig. 322).

Although many species have a minute point to the median lobe when viewed laterally, large distinct single "beaks" are found only in *lyrifer* and *melanderiana*. A "bifurcate" beak is found only in *spinosa* and *biproducta*.

43. Male adminiculum: size of median lobe.

0 = adminiculum with large median lobe, height over one fifth that of total adminiculum.

1 = small median lobe, height only one seventh to eighth that of total adminiculum (Fig. 388).

The size of the median lobe varies throughout the subgenus from one half to one eighth the total size of the adminiculum, but some species in the *diversa*, *sinistra* and *eurystyla* groups have rather small median lobes, and this is considered apomorphic.

44. Male adminiculum: orientation of median lobe.

0 = dorsal margin of median lobe nearly horizontal, at height of dorsal lobes.

1 = dorsal margin of median lobe widely separated from dorsal lobes, with the entire median lobe directed ventroposteriorly (Figs. 65, 322).

State 1 is apomorphic and found in *spinosa*, *biproducta* and *melanderiana*. In *biproducta*, the short dorsal lobes still appear close to the median lobe margin, but the median lobe is clearly projected downward as in *spinosa*.

45. Male adminiculum: carinae of median lobe.

0 = median lobe without line or carina extending from beak, although lobe may have other carinae.

1 = lateral surface of median lobe with line or carina extending dorsally from beak, lobe slightly to strongly expanded laterally (Figs. 8, 259).

Several types of carinae or ridges occur on or near the median lobe (characters 56, 69, 72, 73), and all appear useful for relating species at various levels in the analysis. This character concerns only those extending dorsally from the beak area, which co-occurs in some species with ridges occurring dorsoventrally.

Noted developments include ridges running along posterior margin in some species of the *diversa* group, not dorsoanteriorly as in most species. In most species, the carinae considered

here are only slightly developed, but in *spaldingi* they are greatly developed with the median lobe broad and conspicuous (Fig. 261). The carinae considered here may be homologous to the carinae that flank the posterior margin of the median lobe (Fig. 69) as the positions of both carinae are in close proximity, but never occur together in any single species. Nothing comparable to these carinae are seen outside *Eremotipula*.

46. *Male adminiculum: dorsal processes.*

0 = adminiculum without dorsal processes, cuticle smooth on either side of dorsal spine. 1 = dorsal processes low, mostly rounded (Figs. 7, 8).

2 = dorsal processes present as extended blades (Figs. 269, 270).

Dorsal processes do not occur outside *Eremotipula*, and therefore are considered apomorphic. In addition, the processes in *pellucida* (Figs. 196, 197) are highly distinctive and possibly not homologous with those found in other species of *Eremotipula*. State 2 is a further derivation of state 1 and is seen only in *uitrata* and *auasazi*.

47. *Male adminiculum: emargination of lateral plate.*

0 = outer edge of lateral plate evenly narrowed opposite the dorsal spine.

1 = edge of plate abruptly narrowed opposite the dorsal spine (Fig. 329).

2 = as in 1, but an acute, minute point formed at the corner of the emargination (Fig. 337).

Both states 1 and 2 are found only among species of the *diversa* and *sinistra* group within *Eremotipula*.

48. *Male adminiculum: anterior carina.*

0 = adminiculum smooth anteriorly.

1 = adminiculum anteriorly with a spiny carina on either side (Figs. 259, 251).

State 1 is not seen outside *Eremotipula* and is restricted to the *madina* species group. Although not developed in *impudica* (and coded 0), there is a slight roughness of the cuticle where the carina would be expected to occur.

49. *Male adminiculum: dorsoventral ridges.*

0 = basal (posterior) margin of adminiculum (i.e. below median lobe) straight.

1 = basal margin flanked by a pair of posteriorly-directed, subparallel ridges (Fig. 388).

2 = large, dorsoventral ridge on either side of median lobe (Figs. 419, 434).

Adminicular ridges along the stem are found in the *diversa* group and *spinosa* in *Eremotipula*; nothing similar was seen in the outgroup taxa examined. The ridges are large in *leiocantha* and small in *lyrifer*, *diversa* and *sackei*.

50. *Male adminiculum: basal hooks.*

0 = lateral plates of adminiculum slightly produced basally, but not hook-like.

1 = a distinct hook at the (anterior) base of each lateral plate (Figs. 322, 323).

This is a striking feature found only in the *biproducta* group within *Eremotipula*.

51. *Male adminiculum: base.*

0 = base of adminiculum bisected by a large membranous area, each side extended and attached to the surrounding membrane by a "foot", with body of adminiculum mostly free from sternum.

1 = base of adminiculum expanded laterally as large sclerite, usually with narrow membranous field, each "foot" short, or unrecognizable, body of adminiculum broadly attached to membrane.

See outgroup discussion (character 29).

52. *Female 8S: floor of sternum patterned.*

0 = floor of 8S pale and membranous or solidly sclerotized, pattern not divided and restricted.

1 = brown pattern of sclerotization on floor of 8S, restricted to center and lateral area, forming divided pattern (Fig. 40).

A restricted longitudinal patterning on the floor of 8S is seen only in *Eremotipula* and not in the outgroup taxa examined. Within *Eremotipula*, the patterning is seen in nearly all species where the female is known, absent in only *eurystyla* and *elverae* which have very short hypogynial valves.

53. *Female 8S: inner ridge development.*

0 = major ridge absent (Figs. 41, 42).

1 = slight development of inner (or major) ridge.

2 = well developed (and elongate) ridge (Fig. 40).

3 = ridge well developed, with posterior edge abrupt, outer surface sclerotized.

The pair of ridges on the upper surface of 8S extends forward from near the base of the hypogynial valves (Fig. 40). A pair of ridges is found only in *Lunatipula translucida* among the outgroup

taxa, and occurs in all species of *Eremotipula* (where the female is known).

54. *Female hypogynial valve: dorsal margin sinuous.*

0 = dorsal border of hypogynial valve straight or slightly convex.

1 = dorsal border sinuous, with paler area medially along hypogynial valve.

All outgroup taxa have a straight or slightly convex dorsal border of the hypogynial valve, and the valve itself is usually uniformly sclerotized. In most species of *Eremotipula*, the dorsal border is sinuous, slightly narrower near mid-length and with a lighter colored area. In species with a reduced hypogynial valve size, the valve border is straight in three species (*eurystyla* group) but sinuous in a fourth (*lyrifer*).

55. *Female hypogynial valve: development.*

0 = hypogynial valves of typical tipuline form, relatively elongate and blade-like, ratio of length $8T + \text{cerci} / \text{length } 8S + \text{hypogynial valve} = 1.0\text{--}1.2$; hypogynial valve length/sternum VI length = $1.4\text{--}2.0$.

1 = hypogynial valves short, not blade-like; ratio of length $8T + \text{cerci} / \text{length } 8S + \text{hypogynial valve} = 1.5\text{--}1.7$; hypogynial valve length/sternum VI length = $0.8\text{--}0.9$.

There is much variation in hypogynial valve shape and size in *Lunatipula*, but all near outgroups examined for the species analysis are as in state 0; more distantly related groups do have short hypogynial valves (state 1) such as *Serratipula*, *Odonatisca*, and *Vestiplex*. Within *Eremotipula*, short hypogynial valves appear to be restricted to the *eurystyla* group (where females known). In *Eremotipula lyrifera*, the shortened hypogynial valves are still blade-like.

56. *Female 9T: lateral tubercle.*

0 = lateral edge of female 9T flat or only slightly swollen.

1 = lateral edges of 9T each with well-developed tubercle.

Within *Eremotipula*, a tubercle on 9T is found only in the known females of the *eurystyla* group. It is absent among the outgroups.

57. *Female 10T: longitudinal apodeme complete.*

0 = longitudinal apodeme of female 10T present on posterior half only.

1 = longitudinal apodeme complete.

The apodeme is mostly incomplete in near outgroups (except *Lunatipula lunata*, *L. cava*) but variable within the entire genus *Tipula* (see character 44 of outgroup analysis). All species of *Eremotipula* except *incisa* have a complete apodeme.

58. *Female infra-anal process.*

0 = Setae of infra-anal plate undifferentiated.

1 = Setae of infra-anal plate differentiated; long setae along apical border, very short, dark setae more proximally.

Differentiated setae on the infra-anal process occurs in all species of *Eremotipula* (where the female is known). It is included here as it is variable within the outgroup taxa (see outgroup analysis for fuller distribution, character 49).

59. *Female cerci: laterally expanded.*

0 = cerci compressed, lateral surface not expanded, lateral edge straight (surface not visible ventrally or scarcely so).

1 = cerci with expanded lateral surface (visible from ventral aspect), edge often irregular.

An expanded cercal margin, irregular to toothed in some species, is seen within *Eremotipula* in the species of the *eurystyla* group and *lyrifer* of the *diversa* group. The cercal margin is not expanded among the taxa of the near outgroups, but is seen similarly in the distantly related subgenera of *Tipula*: *Odonatisca*, *Serratipula*, and *Vestiplex* (see outgroup analysis, character 47).

Other characters. Some features were found that were difficult to code, had uncertain homologies, or were difficult to observe. They are listed here for future investigations.

A. *Male 9T subtergal process cuticle surface reticulate.*

A reticulate cuticle on the subtergal process and surrounding ventral plate is found in a number of species of *Eremotipula* (Fig. 89) as well as on the ventral plate in some species of *Lunatipula*.

B. *Male 8S: sclerotized apical margin.*

0 = posterior margin of sclerotization deeply incised medially (Fig. 67).

1 = margin slightly concave or merely undulate (Fig. 421).

2 = margin deeply biconcave (Fig. 348).

Nearly all the species examined in *Lunatipula* s. s. and *Triplicitipula* exhibit state 0. The conditions

in the species of *Eremotipula* were harder to determine, as I had difficulty discerning the exact boundary between the sclerotized and membranous regions of sternum 8. In *incisa*, the sclerotized margin is concave, but because the typical short dark setae are absent from a large medial portion of the sternum, it appears as state 0, as in *melanderiana*. *Tipula larreae* shows a distinct, shallowly concave margin, although there is a paler medial area as in state 0; it probably represents an intermediate condition. A slightly concave margin is found in most species. A number of species show state 2 to some extent, although the distinctiveness of the boundary again varies, even within a species group (e.g., *madina* species group). Three species, *pellucida*, *eurystyla* and *utahicola*, have the margin similar to that in *melanderiana* (Fig. 201). I deleted this character from the analysis due to the difficulty in assigning states.

C. Male 8S: apical band of setae.

0 = band of setae of approximately even width throughout, or widest laterally.

1 = band of greatest width medially, where it extends toward membranous lobe (Fig. 391).

This character has only limited applicability within *Eremotipula* as I found it difficult to determine the state for those taxa where the setae are in two groups, or the setal band is divided medially.

D. Male 8S: microtrichia on membranous lobe.

0 = microtrichia single on or near membranous lobe (Fig. 267).

1 = microtrichia grouped on or near membranous lobe (Fig. 175).

The membranous area between the eighth and ninth sterna is usually covered with single microtrichia in the outgroups, although *Tipula* (*Lunatipula*) *aspidoptera* has microtrichia in groups of six or more. Within *Eremotipula*, the microtrichia are usually single, but occur in small groups in *sinistra*, *artemisiae* and *larreae*. Complications in coding occur when microtrichia are grouped on membrane far laterad of the lobe area, but not near the lobe itself, as in *helferi*, or when the membranous lobe is primitively absent, as in the outgroup taxa or *incisa* (where the microtrichia of the area are also in groups).

E. Male 8S: intersegmental membrane.

0 = membrane between eighth and ninth sterna (membranous lobe area) mostly smooth.

1 = membrane colliculate.

2 = membrane tuberculate (Fig. 242).

This character concerns the texture of the area surrounding the membranous lobe, while the texture of the lobe itself also shows variation within the group. Although extremes can be recognized, I found it hard to assign states, particularly since certain species varied in membrane surface texture. Outgroups were not tuberculate. The strong development of a tuberculate condition in *madina+impudica* and *leioantha+evalynae* lends some support in considering each of these species pairs as monophyletic.

F. Male Adminiculum: lateral plates fused dorsally.

0 = lateral plates not fused together dorsally (Fig. 125).

1 = lateral plates fused together dorsally between the dorsal spine and the median lobe (Fig. 66).

Most species in *Eremotipula* have lateral plates fused dorsally, as in state 1. If not clearly fused, then the plates at least merge with the body of the adminiculum and do not reach anteriorly to the dorsal spine. In *incisa*, *helferi*, *artemisiae* and the *madina* species group, the plates do not meet dorsally, and merge with the adminiculum along the dorsal spine. I considered lack of fusion as plesiomorphic, because of the condition of *incisa* and the subgenus *Lunatipula* s. str. Character 49 is not easily observed, particularly in small species such as *artemisiae*, and differentiating the two states was difficult.

G. Female 10T: apodeme.

0 = apodeme of 10T without pale border (i.e. lighter band of sclerotization).

1 = apodeme with lighter ventral band or border.

A pale border is found in a number of *Eremotipula*, including species of the *diversa* group, *sinistra* group, *madina* group, *pellucida*, *mitrata* and *dimidiata*. It appears absent in *incisa*, *larreae*, *helferi*, *macroantha*, *anasazi*, *kaibabensis* and the near outgroups, and I am unsure in *melanderiana* and *eurystyla*. This feature is hard to observe in cleared specimens unless the 10T is removed, and I was unable to determine intraspecific variation, if any.

H. Female spermatheca surface.

0 = variable surface, smooth or reticulate, scales present or absent but not limited to one half of each spermatheca only.

1 = surface with microscopic scales near base and fine reticulate pattern.

2 = surface with scales extending along one side of bulb, reticulations present.

State 0 is found in outgroups, with most *Ere-*

motipula examined showing state 2. State 1 was seen in *incisa*, *melanderiana* (without reticulations) and *larreae*, and state 0 in *helferi* and *pellucida* (no scales or reticulations) and *eurystyla* and *sinistra* (scales and reticulations).

Table 4. Character state matrix for the species of *Tipula* (*Eremotipula*) and selected outgroup taxa of the genus *Tipula*. The first seven listed taxa (*Platytipula* through *Lunatipula*) were used as outgroups

Character number	10	20	30	40	50	59
<i>Platytipula</i>	000?000000	0?000?0000	0000000000	0000??00??	000000?000	00?0?0000
<i>Labiotipula</i>	00?0010000	0?10300000	0?0000?040	1000??00??	000000?000	0000000000
<i>Triplicitipula</i>	00?1000000	0?000?0000	0?0020?040	0000?000??	000000?000	0000000010
<i>Lunatipula duplex</i>	00?0000000	0?100?0000	0?0020?000	1000?000??	000000?000	1000000000
<i>Lunatipula translucida</i>	00?0000000	0?200?0000	1?0020?000	1100?000??	000000?000	1010000000
<i>Lunatipula bisetosa</i>	00?0000000	0?100?0000	0?0020?000	1000?000??	000000?000	1000000010
<i>Lunatipula lunata</i>	00?0000000	0?100?0000	0?0020?000	1000?100??	100000?000	1000000110
<i>Eremotipula anasazi</i>	0000011010	3010412001	2000200100	1212510100	1000020000	0131001110
<i>Eremotipula artemisiae</i>	0000010010	1010411001	2000200100	1212510100	1000110000	0111001110
<i>Eremotipula baumannii</i>	0000110000	1010213031	2000260141	11103002?0	1010000000	0?????????
<i>Eremotipula biproducta</i>	0000?10010	3020411001	2000290120	121??10110	1101000001	0?????????
<i>Eremotipula byersi</i>	0000010010	1020412001	2100230110	1211600130	1010000100	0?????????
<i>Eremotipula dimidiata</i>	0000010011	?120412001	2010200100	1212510100	1000110000	0131001110
<i>Eremotipula dissipina</i>	0001010010	2020417?01	2000250020	1214910130	1010000000	0?????????
<i>Eremotipula diversa</i>	0000011011	2121416101	2000240120	1214911101	1000101020	0121001110
<i>Eremotipula elverae</i>	0100??????	??????????	??????????	??????????	??????????	?01011111
<i>Eremotipula eurystyla</i>	0000110000	1010312021	2000260040	11100002?0	1010000000	001011111
<i>Eremotipula evalyinae</i>	0000011010	2121416001	3000240120	1214911101	1010001000	0111001110
<i>Eremotipula helferi</i>	0000010010	1000100001	1000271140	1?10000101	1010000000	011011111
<i>Eremotipula impudica</i>	0000010010	1020412001	2100230110	1211600120	1000100000	0111001110
<i>Eremotipula incisa</i>	0001000000	0?10201000	0000280000	1000100100	1000000000	0110000010
<i>Eremotipula jicarilla</i>	0000010010	1010411001	2000200110	1211600100	1010001000	0111001110
<i>Eremotipula kaibabensis</i>	0000010010	3020412001	2010200100	1212510100	1000110000	0131001110
<i>Eremotipula kirkwoodi</i>	1100010000	1010214041	1001261140	11?0200100	1000000000	0?????????
<i>Eremotipula larreae</i>	0000010000	1010202001	2000200110	1100410101	1000000000	0111001110
<i>Eremotipula leiocantha</i>	0000011010	2121416001	3000240120	1214910101	1010001010	0111001110
<i>Eremotipula lyrifera</i>	0000011111	2120416001	3000240120	1214910101	1000101010	0111001111
<i>Eremotipula macracantha</i>	0000010010	1020312001	3000200100	1110410100	1000010000	0111001110
<i>Eremotipula maderensis</i>	1100010000	1010305041	1001261120	11?0200130	1000100000	0?????????
<i>Eremotipula madina</i>	0000010010	1020412001	2000210110	1211600120	1000100100	0111001110
<i>Eremotipula melanderiana</i>	0000000000	0?10202011	2000200100	1100410100	1001000000	0121001110
<i>Eremotipula middlekauffi</i>	1011010010	3010417001	20?0210120	1213510110	1010101000	0?????????
<i>Eremotipula mitrata</i>	0000010010	3120412001	2000200100	1212510100	1000120000	0131001110
<i>Eremotipula pellucida</i>	0000210010	3010206001	1000220120	1212710100	1010010000	0111001110
<i>Eremotipula rogersi</i>	1100010000	1010315041	1001261120	11?0200130	1000100000	0?????????
<i>Eremotipula sackeni</i>	0000011111	2121416101	2000240120	1214911101	1000101020	0111001110
<i>Eremotipula schusteri</i>	0000110010	2020412001	2000210120	1212710100	1000010000	0?????????
<i>Eremotipula sinistra</i>	1011010010	1010417001	2000210120	1213810110	1010101000	0121001110
<i>Eremotipula spaldingi</i>	0000011010	2020412001	2000230110	1211600120	1000100100	0121001110
<i>Eremotipula spinerecta</i>	0000010000	1010100001	2000271130	1000000100	1000000000	0?????????
<i>Eremotipula spinosa</i>	0000010010	3020413001	2000220120	1213810110	1101000021	0?????????
<i>Eremotipula utahicola</i>	0000010000	1010213031	2000260141	11103002?0	1010000000	0?????????
<i>Eremotipula woodi</i>	0001010010	3010417001	1000210120	1213810110	1010000000	0111001110

Parsimony Analyses

Two main sets of analyses were run, treating all characters as non-additive (unordered) or additive (ordered). As noted above, 17 characters had multiple states and 42 characters had binary states. Because of the uncertainty of the close outgroups for *Tipula* (*Eremotipula*), even with the outgroup analysis presented earlier, I chose to include a number of outgroups in the analysis, with simultaneous analysis of all terminal taxa, therefore testing monophyly of *Eremotipula* and determining polarity of the character transformations based on the entire data set (Swofford & Begle 1993, Nixon & Carpenter 1993). Although results for all analyses are presented, character changes and character support for clades are discussed comprehensively for the non-additive (unordered) character analyses only. *Eremotipula elverae*, known only from the female stage, was deleted from the final analyses due to the lack of information on male characters of the species but its possible relationships are discussed in the following section on the *eurystyla* group.

Analysis 1. The large size of the data matrix prevented exact search algorithms from being used. Characters were treated as additive (ordered), and analyzed through a heuristic search algorithm in PAUP with the following parameters: ADDITION = simple, HOLD = 5 trees at each step, BRANCH SWAP = Tree-bisection-reconnection (316,291 rearrangements tried), MULPARS, and zero length branches collapsed. The analysis resulted in 12 trees of length = 262, consistency index (CI) = 0.412 and retention index (RI) = 0.791. The strict consensus tree (Fig. 17) shows *Eremotipula* as a monophyletic group, with lack of resolution within *Eremotipula* in the *kaibabensis* group (reading from top, *anasazi* through *mitrata*), the placement of *eurystyla*, *helferi* and *spinirecta* in the *eurystyla* group (*baumanni* through *spinirecta*), and the placement of *jicarilla*.

Successive approximations character weighting (SACW) after two heuristic searches found three trees, CI = 0.70, with no topologies identical to the 12 trees in the original starting set. The strict consensus tree (Fig. 18) shows lack of resolution only in the placement of the *biproducta* group (*biproducta*, *spinosa*).

Analysis 2. Characters were treated as non-additive (unordered), and analyzed with multiple

replications of the heuristic search algorithm in PAUP, with the following parameters: ADDITION = as is, simple, closest and random = 10, HOLD = 10 trees at each step, BRANCH SWAP = Tree-bisection-reconnection (1,334,404 to 23,021,308 rearrangements tried), MULPARS, and zero length branches collapsed. To test the effectiveness of finding the most parsimonious solution for the data set, particularly to avoid remaining in an "island" of trees, the addition parameter methods were varied and HOLD was set high before inputting into branch swapping. Even by changing the addition parameter, all analyses resulted in the same 57 trees of length = 201, consistency index (CI) = 0.53 and retention index (RI) = 0.77. The 57 trees were filtered to 32 trees by filtering out less resolved trees when a more fully resolved tree with the same topology was available. The strict consensus tree (Fig. 19) shows *Eremotipula* as a monophyletic group, as with the additive character, parsimony analyses results Analysis 1). Lack of resolution among the trees occurred due to alternative placements of *artemesiae*, *disspina*, *pellucida*, *madina* group (reading from top, *byersi* through *spaldingi*) and lack of resolution within the *madina* group. Among all 32 trees, there are a total of 16 variable components (Figs. 21–32).

The 16 components were scored for number of unique unreversed characters supporting each relevant node (Table 5), adapting a method Kluge (1989) used for comparing congruence from different datasets. These synapomorphies may constitute stronger evidence for monophyly than those characters which are never found as unique or unreversed in any most parsimonious resolution. Specified trees featuring the combined highest valued components ((A1 or A2) + B2 + C2 + (D1, 2 or 3) + F2) are not represented among the 32 original, most parsimonious trees, but require an additional step (202 steps).

Successive approximation character weighting yielded six trees after two heuristic searches, with CI = 0.70, RI = 0.87. All variation in the topology among the trees was found in the *madina* group only (Fig. 20). Of the six trees, two of these trees were just less resolved replicates of two fully resolved trees and one tree lacked characters in the variable node support due to missing data and were discarded; the remaining three trees had an identical topology to three trees in the original 32 trees starting set (components B1, B2, B5; Figs. 22, 25, 28). The strict consensus tree from these 3 trees

shows lack of resolution only for four taxa within the *madina* group (*byersi* through *spaldingi*,) with placement of *jicarrilla* stable as the sister taxa to rest of the *madina* group species.

Bootstrap Analysis. A bootstrap analysis was run as a measure of statistical confidence in the hypotheses of relationships resulting from the non-additive character, parsimony analysis (see above). The analysis was run with 100 replications, with MAXTREE = 100. Unfortunately, the maximum number of trees was exceeded on every replication but attempts to increase MAXTREE caused higher numbers of trees to be saved and exceeded the memory limitations of the computer. The bootstrap values over 50% are shown in Fig. 35 and show high confidence for parts of the tree. The values for the variable components are given in Table 5. Based on these values, the component with the highest percentage from each component group were chosen; the trees formed by a combining of these components (A1 + (B1, B2, B4 or B5) + C2 + D1 + F2) were not among the original 32 min-

imum length trees, but require an additional step (202 steps).

"Near-minimal" trees. Support for the hypothesis of relationships in the minimal length trees was also investigated by noting groups in optimal trees which were also supported in suboptimal trees (Swofford & Begle 1993). The parameters of analysis 2 were replicated and included setting the parameter KEEP = 202 or less, which retained all optimal trees and those trees one step longer in memory. The search ended prematurely due to a lack of computer memory but retained 1700 of the trees. The strict consensus tree from this admittedly partial set of trees is shown in Fig. 36. Notably, *incisa*, *melanderiana* and *larreae* are retained as the most basal species, with all other species in an unresolved grouping. Within this unresolved group, the *eurystyla*-, *biproducta*-, *diversa*-, and *sinistra*-species groups are entirely or in part retained as monophyletic, with retention of basal lineage structure (*incisa*, *melanderiana*, *larreae*, remaining species clade).

Table 5. Comparison of measures of character support for 16 variable components from phylogenetic analysis of *Eremotipula* (non-additive character set).

Component no.	No. of unique unreversed synapomorphies	Bootstrap value (%)	Presence in successive approximation (s.a.) trees (nonadditive analysis)
A1	0	47	x
A2	0	6	
B1	1 + 1 + 0 = 2	69/29/44	x
B2	1 + 1 + 1 = 3	69/13/29	x
B3	0 + 1 + 0 = 1	15/39/44	
B4	1 + 1 + 0 = 2	69/22/44	x
B5	1 + 1 + 0 = 2	69/39/44	
C1	1	28	x
C2	2	45	
D1	1	25	x
D2	1	9	
D3	1	4	
F1	0 + 0 = 0	2	
F2	2 + 1 = 3	45	
F3	0 + 0 = 0	25	x
F4	2 + 0 = 2	9	
Preferred tree composition	A1/A2;B2;C2; D1/D2/D3;F2	A1; B1/B2/B4/B5; C2;D1;F2	A1;B1/B2/B4; C1;D1;F3
Topology in original tree set?	NO	NO	YES
Length of preferred tree? shortest = 201	202	202	201 (85975 as s.a. tree)

Choosing among multiple, equally parsimonious trees. Both sets of phylogenetic analyses, using non-additive and additive character data, provide a number of hypotheses of species relationships for *Tipula* (*Eremotipula*). For analysis 2, which treated characters as non-additive, there are 32 equally valid hypotheses (i.e. equal length trees), not including those additional 25 that were filtered. Three measures were used to attempt to choose among the 32 competing equal length trees resulting from analysis 2: successive approximation (a posteriori weighting); number of unique, unreversed synapomorphies and for additional comparison, highest bootstrap values. Although all measures listed have their critics, bootstrap values, in particular, are controversial, and Sanderson (1989) cautions against undue emphasis being placed on the interpretations of bootstrap values. Comparative results for the 16 variable components and 3 measures are given in Table 5. The three measures did not converge on the same set of components. The use of the number of unique, unreversed synapomorphies and highest bootstrap values both determined a common set of components as best supported: A1 or A2, B2, C2, D1 and F2 (maximized 9 unique, unreversed synapomorphies). A tree combining these components does not match any tree in the original set; at 202 steps, it is a single step longer than any tree in the original, most parsimonious tree set. The additional step arises from differences in optimization of characters 43 and 45, both homoplasious.

The three successive approximation trees did contain a combination of components which matched the topology of those in the original set of trees, but incorporated components C1 and F3, which do not maximize the number of unique unreversed synapomorphies nor coincide with highest bootstrap values. Component C2, placing *dis-spina* as a member of the *diversa* group, and components F2 and F4, placing the *madina* group as more closely related than *macracantha* to the other "derived" species groups, are more convincing to me based on character evidence, in particular, the unique unreversed synapomorphies. As such, I prefer the tree figured in 21 as the best compromise as it incorporates components C2 and F4 and explains seven of the characters in the conflicting components as unique and unreversed. By comparison, the maximum number of characters treated as unique and unreversed for these components is eight (components A1 or A2,

B2, C1, D1, 2 or 3, F2), with the successive approximation trees at five. Emphasis on other character data will lead to a different set of preferred topologies.

DISCUSSION OF SPECIES LEVEL ANALYSES OF EREMOTIPULA

Monophyly of Eremotipula. Although the subgenus *Tipula* (*Eremotipula*) was thought to be monophyletic based on the preliminary outgroup analysis presented earlier, the ingroup analysis confirms this by showing a large number of synapomorphies shared by these species. If *incisa* is included in the subgenus, as followed in this work, 5 characters indicate monophyly of the subgenus, with closely-attached lateral plates of the male adminiculum (character 38) a uniquely derived synapomorphy, and male subtergal process (character 15), ventral plate shelf (character 17), and in the female, patterning (character 52) and ridge development (character 53) of the female eighth sternum, all showing little homoplasy. Possibly a synapomorphy of *Eremotipula* is character 41, the development of a large, mostly lightly-sclerotized median lobe of the male adminiculum found in nearly all the species. Many outgroup taxa have a small, nearly hook-like, median lobe (if it is at all recognizable), although the lobe in some species of *Lunatipula* (e.g., *lunata*, *rabiosa*) appears homologous to that in *Eremotipula*. The bootstrap value for this node is 74% (Fig. 35) and the subgenus remained monophyletic even when suboptimal trees were examined (Fig. 36). [Character 51, although plotted at this node, is included due to the inclusion of multiple outgroups and may be a symplesiomorphy; see the outgroup analysis for a complete look at this character].

Even stronger support of monophyly is seen when all species except *incisa* are considered. Nine characters indicate support, including 3 which are unique and unreversed: male A9S lobe membranous distally and with thickened, laterally directed setae (20, 21) and male outer basal lobe shape (35). Other distinctive features with little homoplasy are the anterior extension of the male outer dististyle (28), female hypogynial valve margin (54) and female tergal apodeme (57). The bootstrap value is high confidence at this node (99%, Fig. 35) and the clade remained monophyletic even when suboptimal trees were examined (Fig. 36)

Although weaker support exists for inclusion of *incisa* into *Eremotipula*, I have transferred *incisa* from *Lunatipula* to *Eremotipula*, recognizing its shared male and female features, and its close relationship with the other species in *Eremotipula*. It should be noted that several other species formerly in *Lunatipula* and also relatively basal in the phylogeny, *kirkwoodi* and *spinerecta*, were not recognized previously as species of *Eremotipula* but are transferred here now.

Species group relationships. Beyond the initial lineages just discussed, the two basal species, *melanderiana* and *larreae*, are similar in aspects of the ninth tergum, outer basal lobe and eighth sternum, but there are no synapomorphies to support a sister species relationship. In particular, the putative synapomorphies of two features of the male eighth sternum, the complete setal band (6) and derivation of a membranous lobe (15, this area only slightly swollen in *melanderiana*), are important in determining that *larreae* is clearly more related to the other, more derived species in the subgenus. The membranous lobe feature is unique and unreversed and the complete setal band is unreversed and found only elsewhere in *Labiotipula* among the near outgroups. This position of *larreae* is maintained in suboptimal trees (Fig. 36) but below the 50% bootstrap level (Fig. 35).

The grouping of the *eurystyla* species group with the remainder of species (termed here "derived species groups") is supported by the absence of microtrichia on the male subtergal blade (character 16), and rotation of the male outer basal lobe (character 33, reversed in one species of *eurystyla* group), but both features reversed elsewhere within the subgenus. The monophyly of the *eurystyla* group is strongly indicated by the male basistyle projection shape (character 26), female shortened hypogynial valve (character 55) and ninth tergum tubercle (character 56), all unique unreversed synapomorphies, and this strong character support is reflected in the bootstrap value (56%) and retention of the group even when suboptimal trees are examined (Fig. 36). In addition, the male inner dististyle lacks a crest, there is a reduction of the ridges on the beak (most ingroup and outgroup taxa possess both) and the females, where known, have the cerci laterally expanded and toothed. The female characters, particularly the toothed cerci and shortened hypogynial valves are suggestive of a deep-boring

oviposition, as seen in the subgenera *Vestiplex* and *Odonatisca* (Hemmingsen 1956).

The *kirkwoodi*, *eurystyla*, and *helferi* subgroups, are noted within the *eurystyla* species group as evidenced by strong character support, high bootstrap values and consistency of the topology even in suboptimal trees. A single unique, unreversed character, the expansion of the male basistyle posterior edge (character 27), supports a relationship between the *helferi* and *kirkwoodi* subgroups (Fig. 33). The monophyly of the *kirkwoodi* subgroup is evidenced by four unique, unreversed features, including wing pattern (character 2), inner lobe of the male basistyle (character 24) and shape of the male outer basal lobe (character 35). Within this subgroup, *maderensis* and *rogersi* appear as sister species due to a number of features, most notably the male ventral lobe shape of the 9T (character 17) and spiny dorsal lobes of the male adminiculum (character 39). The species *helferi* and *spinerecta* are sister species as evidenced by a number of male characters, including reduction of the subtergal blade to a minute point (character 15) and the basistylar lobe shape (character 26). The *eurystyla* subgroup appears monophyletic as supported by the uniquely shaped male adminicular dorsal lobes (character 38), and *baumanni* and *utahicola* are sister species as evidenced by three unique male characters, including the inner dististyle lamellae (character 30) and shape of the outer basal lobe (character 35). The species *elverae*, known only from the female stage and deleted from the analysis, certainly belongs in the *eurystyla* group based on characters 54, 55, 56, and 59. From there, it could be placed near the *eurystyla* subgroup due to lack of eighth sternal patterning (character 52), *helferi* subgroup (on overall similarity) and the *kirkwoodi* subgroup due to a pale r_5 wing cell (character 2). Its addition adds a single step to overall treelength.

The monophyly of the "derived species groups" (Fig. 21) is supported by four male features, none unique and/or unreversed features. These are loss of the thickened lateral seta on the 8S (character 9), extended dorsal lobes of the 9T (character 13) (seen elsewhere only in *Lunatipula translucida* among the near outgroups), a rod-like STP (character 15) and short dorsal processes on the adminiculum (character 46). The adminicular processes, although unique, are lost subsequently in 3 species groups, and appear modified further in several other species. In particular, the huge

processes of *pellucida* may not even be homologous to those in *kaibabensis* and others.

In all analyses, the placement of *macracantha* is isolated among these derived species groups but the character evidence conflicts whether it or the *madina* group is most closely related to the remaining species, as shown in components F1–4 (Figs. 21–24). Based on the number of unique, unreversed synapomorphies, components F2 and F4 have the strongest support with two characters, with the *madina* group shown as more closely related to the other derived species groups than is *macracantha* (Figs. 21, 23). These characters are both of the male outer basal lobe, the posterior direction (character 32) and setal arrangement in loose line (character 34); in addition the male subtergal process is elongate with a lacinate margin (character 15), this state is reversed only in *pellucida*. Median lobe size of the male adminiculum (character 43) is the only support in component F4 for relating the *madina* group to a subset of these derived species groups, and this entails that the male dististyle be redeveloped in size (character 29). Support for the *madina* group as a sister group to the remaining taxa, as in component F2, is stronger, including character 34(1) (Fig. 23). The placement of *macracantha* along a more derived branch than the *madina* group (Fig. 24) includes male characters: character 46 (above), reduction of the crest (character 29) and lengthening of the 9T lobes (character 13-2). The bootstrap value for F2 was highest among the four F components, and the SACW trees from analysis 1 (additive) also support F2; the SACW trees resulting from analysis 2 (non-additive) support component F3.

The monophyly of the *madina* group is indicated by several synapomorphies (Fig. 21), with one, male outer basal lobe shape (character 34-2), unique and unreversed. A monophyletic *madina* group is maintained in the bootstrap analysis (62%) but the group dissolves in the suboptimal analysis. Resolution of the relationships within the *madina* group are problematic, due to conflicting evidence from several unique characters, although *jicarilla* is supported as the sister species to the rest, due to its lack of male characters 26, 39 and 48. Of the relationships of the remaining four species, six separate components are identified from analysis 2. One of these is discarded as the support for a sister species pair relies on a female character not known for one of the species pair. The remaining 5 components are in Figs. 22,

25–28. Based on number of unique, unreversed characters, component B2 (Fig. 22) is the best supported with three male characters: adminiculum dorsal lobe teeth (character 39), basistylar spine (character 26) and A9S lobe size (character 22). The other 4 topologies group *spaldingi* and *madina* as sister taxa (Figs. 25–28), relying solely on various homoplasious characters (character 22, 45, 48). The bootstrap analysis supported *jicarilla* as the sister species to the rest (69%), but was not decisive among the remaining 4 species. All variation in the SACW for analysis 2 resided within this group, supporting components B1 (Fig. 25), B2 (Fig. 22) and B4 (Fig. 27); the SACW run of analysis 1 (additive data) supported component B2.

Returning to the main cladogram (Fig. 21), *artemesiae* has been placed with either the *kaibabensis* or *madina* species groups, components A1–A2 (Figs. 21, 22), both based on weak characters. Support for *artemesiae* as the sister species to the *kaibabensis* group relies best on the male outer basal lobe shape (character 35). Support for *artemesiae* as the sister species of the *madina* group relies on reversals in two characters (character 13, 17) in *artemesiae* and *jicarilla*, then re-reversals in the remaining *madina* group species. SACW supports *artemesiae* with the *kaibabensis* group, and this is also seen in the bootstrap analysis (47%). Note that analysis 1 (additive characters) places *artemesiae* with the *kaibabensis* group in the original set of trees, but it becomes a sister species to much of the derived species groups after SACW (Fig. 18).

The monophyly of the *kaibabensis* group is indicated by a single unique, unreversed synapomorphy (Fig. 22), development of female 8S ridge (character 53), with additional support from an elongate membranous lobe of the male 8S (character 11), which shows parallel development. Bootstrap analysis excludes *anasazi* from the group (Fig. 35) and the suboptimal analysis dissolves the group (Fig. 36), but both parsimony and SACW analyses confirm the species group. The pairing of *mitrata* with *anasazi*, and *dimidiata* with *kaibabensis*, are based on a single unique unreversed synapomorphy each. For *kaibabensis* and *dimidiata*, this is a well-developed projection of the dorsomedial border of the male basistyle (character 23). Since smaller projections occur in most of the species of this species group and also *schusteri* (but not *pellucida*), this character may actually circumscribe a

larger group than just *kaibabensis*+*dimidiata*. Other probable synapomorphies (not used in the analyses) include the ventral flange along the medial margin of each dorsal lobe of the ninth tergum, and an expansion of the subtergal process near the base. *Tipula mitrata* and *anasazi* are clearly sister species (Fig. 22), with the extended dorsal processes of the adminiculum (character 46–2) unique within the subgenus. The presence of shortened outer basal lobes in both species, although not considered in the analysis, probably also represents a synapomorphy.

The species *schusteri* is consistently placed as the sister species of the remaining species groups, based on further reduction of the crest size (character 29). Although never considered a sister species of *pellucida*, the two species both possess the same outer basal lobe shape (character 35) and development of the medial margin of the 8S (character 5, seen elsewhere only in the *eurystyla* group). The placement of *pellucida* has three possibilities (components D1–D3, Figs. 21, 31, 32), reflective of its highly autapomorphic male genitalia and subsequent difficulty in making some homology decisions. Support for component D1 and D2 relies on the elongate membranous lobe of male 8S (character 11) and male basistylar lobe (character 26, subsequently modified in all other species except *spinosa*). Support for component D3 is the broad flat lobe of the male 9T ventral plate (character 17), seen elsewhere only in the *diversa* group (except *dissspina*). SACW from both analyses favor component D1, placing *pellucida* as the sister species to the *diversa*, *biproducta* and *sinistra* groups.

A single unique, unreversed synapomorphy, the line of setae on medial ridge of male OBL (34), supports the monophyly of the remaining species groups (*diversa*, *sinistra* and *biproducta* groups, Fig. 21). Within this, the position of *dissspina* is unresolved. Two unique, unreversed synapomorphies found in the male outer basal lobe, extended blade-like shape (character 35) and line of setae along upper ridge (character 34), support *dissspina* as a member of the *diversa* group (component C2, Fig. 30). In addition, they share a broad, flattened membranous lobe of the 8S in the male (character 11). Support for *dissspina* as the sister species to the *sinistra* and *biproducta* groups (component C1) is less convincing (Fig. 29), as the two characters, abdominal setae (character 4) and male ventral plate lobe shape (character 17), are seen only in *dissspina*

and the *sinistra* group, and then must be reversed in the *biproducta* group. The bootstrap value for component C2 is near 50%, and this component is seen in the analysis 1 and SACW (Figs. 17–18). Component C1 is seen in the SACW of analysis 2 results (Fig. 20).

The monophyly of the *diversa* group, including *dissspina*, has been mentioned. The group's monophyly, excluding *dissspina*, is also well supported by characters (Fig. 30) in all analyses and with a high bootstrap confidence value (97%). All species possess an elongate basistylar spine (character 26), unique and unreversed within the subgenus, and several other male characters showing limited reversal or parallelism such as 9T dorsal lobe shape (character 14), glabrous membranous lobe of the 8S (character 12), loss of lateral sclerites of the 8S (character 7) and striate dorsal lobes of the adminiculum (character 47). The species *leiocantha* and *evalynae* are extremely similar, but not supported as sister species in this analysis; they do share a presence of tuberculate cuticle surrounding the membranous lobe. This feature was not used in this analysis but showed widespread homoplasy in an earlier analysis (Gelhaus 1989). It is not found elsewhere among the *diversa* group and may indicate a sister species relationship of the two species. The basal ridges of the male adminiculum (character 49), seen in *leiocantha* and *lyrifera*, and in a different, presumed homologous, form in *sackeni* and *diversa*, support an inclusive clade of these four species without *evalynae*. Isolated setae (character 10) and loss of sclerites (character 8) in the male 8S, possibly related characters, indicate a close relationship of *lyrifera*, *diversa* and *sackeni*. The sister species relationship of *diversa* and *sackeni* is best supported by the line of the ventral plate lobe (character 18), but also due to the aforementioned adminicular ridges (character 49) and convex margin of the inner dististyle (character 37). This latter feature, found also in *evalynae*, differs dramatically in size between *evalynae* and these two species, and probably indicates non-homology. Character 21–3, pale setae of A9S, is problematic as a basal synapomorphy, as it requires a re-development of thick, dark setae of A9S within the group.

The sister group relationship of the *sinistra* and *biproducta* species groups is supported (Fig. 34) by the truncate dorsal lobes of the male adminiculum (character 39), unique and unreversed, as well as outer basal lobe shape (character 35) and shape of

membranous lobe (character 11). Support for the *biproducta* species group as monophyletic (Fig. 34) comes entirely from characters of the male adminiculum, including a bifurcate beak (character 42), basal hooks (character 50), both unique and unreversed, and orientation of median lobe (character 44). The relationship is supported in all analyses, with a bootstrap confidence of 96%. The *sinistra* species group is less well supported, with no unique unreversed features, but is maintained in all analyses with a relatively high bootstrap value of 76%. The sister species relationship of *sinistra* and *middlekauffi* has high confidence, due to distinctive wing (character 1) and leg (character 3) coloration patterns and an emarginate adminiculum (character 47, Fig. 34). The relationship is seen in all analyses, including in suboptimal trees, and bootstrap confidence of 96%. The similar membranous lobe of *woodi* and *middlekauffi* must be considered symplesiomorphic.

SYSTEMATICS OF *EREMOTIPULA*

CHECKLIST

The following is a checklist of species of *Eremotipula* arranged alphabetically. Valid species are in bold with synonyms in italics. The name in parentheses after each species name is the original genus in which the specific name was proposed. The type material for all species-level names was examined during this study.

Subgenus *Eremotipula* Alexander 1965

anasazi Gelhaus (*Tipula*) **new species**
artemisiae Gelhaus (*Tipula*) **new species**
baumanni Gelhaus (*Tipula*) **new species**
biproducta Alexander 1947 (*Tipula*)
byersi Gelhaus (*Tipula*) **new species**
dimidiata Dietz 1921 (*Tipula*)
coconino Alexander 1946 (*Tipula*) **new synonym**
disspina Gelhaus (*Tipula*) **new species**
diversa Dietz 1921 (*Tipula*)
elverae Gelhaus (*Tipula*) **new species**
eurystyla Alexander 1969 (*Tipula*)
evalynae Gelhaus (*Tipula*) **new species**
helferi Alexander 1965 (*Tipula*)
impudica Doane 1901 (*Tipula*)
albocincta Doane 1901 (*Tipula*) **new synonym**
incisa Doane 1901 (*Tipula*)
flavicomma Doane 1912 (*Tipula*)
kausensis Alexander 1918 (*Tipula*) **new synonym**
ericiensis Alexander 1942 (*Tipula*) **new synonym**

incisa ssp. *queres* Alexander 1946 (*Tipula*) **new synonym**

incisa ssp. *picturata* Alexander 1961 (*Tipula*) **new synonym**

jicarilla Gelhaus (*Tipula*) **new species**

kaibabensis Alexander 1946 (*Tipula*)

kirkwoodi Alexander 1961 (*Tipula*)

larreae Gelhaus (*Tipula*) **new species**

leiocantha Alexander 1959 (*Tipula*)

lyrifera Dietz 1921 (*Tipula*)

carunculata Alexander 1945 (*Tipula*) **new synonym**

macracantha Alexander 1946 (*Tipula*)

maderensis Gelhaus (*Tipula*) **new species**

madina Dietz 1921 (*Tipula*)

melanderiana Alexander 1965 (*Tipula*)

middlekauffi Alexander 1965 (*Tipula*)

mitrata Dietz 1921 (*Tipula*)

pellucida Doane 1912 (*Tipula*)

clara Doane 1901 (*Tipula*; preoccupied by Kirby 1884)

pyramis Doane 1912 (*Tipula*)

rogersi Gelhaus (*Tipula*) **new species**

sackeni Gelhaus (*Tipula*) **new species**

schusteri Alexander 1965 (*Tipula*)

sinistra Dietz 1921 (*Tipula*)

spernata Dietz 1921 (*Tipula*) **new synonym**

spaldingi Dietz 1921 (*Tipula*)

spinirecta Alexander 1947 (*Tipula*)

spinosa Gelhaus (*Tipula*) **new species**

utahicola Alexander 1948 (*Tipula*)

woodi Alexander 1948 (*Tipula*)

Subgenus *Eremotipula* Alexander

Tipula (*Eremotipula*) Alexander 1965: 340. Type species: *Tipula* (*Eremotipula*) *impudica* Doane 1901, by original designation.

Diagnosis.—Males of *Tipula* (*Eremotipula*) can be distinguished from other *Tipula* by these three synapomorphies: 9T with a median STP, usually elongate and compressed, with dorsal margin serrulate and apex pale (Figs. 2, 3); ventral plate of 9T with a pair of curled, lateral shelves, each with a posteriorly-directed lobe (Fig. 235, reduced in *helferi*); adminiculum with closely appressed lateral plates, merging with paired dorsal lobes (Figs. 7, 8). Other distinguishing features are: ventral lobe of A9S membranous distally with straight, usually short, thickened, laterally directed setae (Figs. 77, 342, lobe sclerotized with long and twisted setae in *incisa*). Outer dististyle usually extended anteriorly into a beak (Figs. 2, 424), outer basal lobe of ID usually directed posteriorly (Fig. 4), less often dorsoposteriorly, or dor-

sally (in *incisa* only), a median membranous lobe nearly always present between 8S and 9S (Fig. 2).

Females of most species of *Tipula* (*Eremotipula*) can be distinguished from other *Tipula* by a set of synapomorphic features of the hypogynial valves and associated 8S: distinctive sclerotized pattern on the inner floor of the 8S at the base of the valves (Fig. 40); slightly to well developed pair of ridges along upper surface of 8S extending forward from base of valves (Fig. 72); sinuous dorsal border of each blade, with medial area of blade distinctly pale (Fig. 71), straight border and uniformly dark in *incisa*, (Fig. 58) reduced in size and margin straight in *elverae*, *eurystyla*, and *helferi*; also a complete longitudinal apodeme of 10T (Figs. 117, 128, not complete in *incisa* Fig. 56); and spermatheca with scales present at base or along one side only. In *eurystyla*, *helferi* and *elverae* with tubercle on 9T laterally, cerci expanded laterally, and hypogynial valves vestigial.

Description.—*Body length*: total range: male 11–22 mm; female 15–30 mm. *Body coloration* brown to yellowish brown; one species, (*mielandriana*), distinctly dark reddish-brown. *Head*: Vertex and postgena pruinose. Rostrum mostly shiny, with some pruinosity dorsally and near base. Vertex usually with brown longitudinal dorsomedial line. Antennal length: male 4–6 mm, female 2–4 mm. Scape and pedicel yellowish brown, flagellomere I yellowish brown with brown on ventral half, remainder of flagellomeres dark brown. Nasus present or absent, development varying within a species. *Thorax*: Pruinose overall; postpronotum, anterolateral corner of prescutum, other membranous areas and suture between meron and katepimeron pale. Presutural scutum usually with two pairs of parallel, longitudinal, distinct to indistinct, brown to dark brown stripes. Postsutural scutum with two pairs of distinct to indistinct brown spots; median pair immediately behind lateral stripes on presutural scutum. Scutellum usually with longitudinal, median brown line. Mediotergite with line extending anteriorly from posterior edge to middle of notum. Pleural region densely pruinose. Setae on katepisternum dark brown to yellowish brown, 0–12 in number and varying widely within a species, located along anterior margin of episternum at midlength. Meron sometimes with 1–6 light brown to brown setae near posterodorsal corner, setae often absent. Metakatepisternum with few to many setae, ventral-most setae darkest. *Legs*: Coxae con-

colorous with pleura; remainder of legs yellowish brown. Femora in most species with brown to dark brown subapical ring (= femoral ring). Apex of each tibia often darkened. Tibial spur formula = 1.2.2. *Wing*: Male 11–20 mm long; female 12–22 mm long. Membrane light brown or gray, stigma usually brown, scarcely darker than ground color in *sinistra* species group and *pellucida*. In most species, clear areas nearly surrounding stigma, and extending along cord and into discal, m_3 and m_4 cells, with pale streaks along A_1 and in cell a_1 . *Abdomen*: Terga overall yellowish brown and shiny, tergum 1 slightly pruinose. Dark brown patches dorsally and sublaterally along terga 1–6, sometimes on terga 1–8, occasionally forming a continuous line; markings absent in some species. *Hypopygium*: *Ninth tergum* (9T): Small, ratio of length 9T/BS = 0.32–0.60. Tergum with two dorsal lobes, a posteriorly directed process arising ventrally from medial area of tergum (= subtergal process, STP) and two ventral lobes (Figs. 2, 3, 234, 235). Dorsal lobes subparallel (Fig. 383) to divergent (Fig. 60), often elongate, ratio of L/W (at base) = 0.17–2.0; of various shapes, apices usually acute to subacute, (lobes absent in *helferi*, Fig. 120). STP short to elongate (Figs. 49, 316), often compressed, with width narrowing to apex; ratio of length STP/9T = 0.1–1.0 (0.05 in *helferi*); when elongate, blade pale in apical one fifth to one half, dorsal margin serrulate to lacinate. Posterior margin of 9T beside dorsal lobes usually shallowly to deeply emarginate. 9T with sclerotized ventral plate, reflexed from posterior margin and including STP (Fig. 235). Curved, smooth shelf beneath either side of plate with extension forming ventral lobe (shelf lacking in *helferi*). Inner margin of reflexed plate thickened with a pair of anterior processes (Fig. 61). Ventral lobes of various sizes and shapes (Figs. 75, 325, 384), some exposed in dorsal view of tergum. *Ninth sternum* (9S) (+ *basistyle*, BS): Basistylar suture complete to incomplete, but reaching dorsal margin of 9S (Fig. 2). BS a complete ring dorsally (Fig. 226), fused anteriorly to “spangen 2” (sp2), dorsomedial margin slightly irregular outside, smooth and rounded inside. Sp2 a large, triangular sclerite with curled lateral edges (Figs. 226, 302), convergent in *helferi* (Fig. 123); “spangen 1” (sp1) attached by membrane to inner margin of BS (not to sp2, Fig. 226). Dorsolateral edge of BS, opposite posterior condyle of ID, usually produced into small to large process, often as small to large spine (Figs.

94, 427). Appendage of ninth sternum (A9S) usually distinctly divided into dorsal and ventral portions (= dorsal and ventral lobes, Fig. 2). Dorsal portion (= dorsal lobe) low and broadly attached, secondarily divided in *incisa* (Fig. 44), with moderate to long, erect setae. Ventral portion (= ventral lobe) pendulous, attached to membrane overlying base of adminiculum, usually with basal swelling with setae (Figs. 7, 342); remainder of ventral lobe membranous and extended distally, without setae but pilose (lobe entirely circular and sclerotized in *incisa*, Fig. 44). Setae on ventral lobes moderately thickened, yellowish or reddish brown and directed laterally in most species, e.g., *sinistra* (Fig. 342), sometimes few in number and greatly thickened (Fig. 178) or long, erect, slender and directed dorsally (Fig. 386). A membranous protuberance, with dense microtrichia, located below A9S in *eurystyla* (Figs. 92, 93), *melanderiana* (Fig. 68) and *utahicola* (Fig. 111). *Outer dististyle* (OD): Base curved laterally around inner dististyle, extended anteriorly into short to elongate beak (Fig. 2), beak rarely absent. *Inner dististyle* (ID): Base with a pair of similar condyles (Fig. 4), scarcely distinguishable in *incisa* (Fig. 45). Upper and lower beaks approximate, blackened anteriorly; ventral surface of upper beak and apex of lower beak with weak to strong ridges (Fig. 292), sometimes absent. Upper beak dorsally with broad, flat shelf dorsally (Figs. 5, 6), with many fine longitudinal striations and short pale inconspicuous hairs. Crest (Figs. 4, 5) present in all species except those of *eurystyla* group; usually pale, sometimes extending along upper beak with groove between crest and beak (e.g., *impudica*, Fig. 227). Dorsal margin of crest distinctly to indistinctly serrulate, (Fig. 76). Crest with scattered spinules in most species (Fig. 303), rarely tuberculate (Figs. 45, 64). Mesal surface of anterior half of ID convex, with setae along ridge increasing in length toward base (Fig. 5). Basiconic pegs 6–30 in number, usually in oval to reniform group, at or near base of outer basal lobe (Figs. 5, 6). Lateral surface of ID concave and smooth, with irregular row of subequal setae extending from lower beak to near apex of outer basal lobe. Outer basal lobe a short to elongate blade (Figs. 2, 3) small and rounded in *eurystyla*, concave to flattened laterally, directed posteriorly in most species (Fig. 4), L/W = 1.0–4.2; ridge on lateral surface in some species, apex of OBL variable. Mesal surface of basal half of OBL with abundant long setae and

patch of fine hairs (Figs. 5, 6). *Adminiculum*: Divided by pale area at base (Fig. 7). Lateral plates (Fig. 8) closely appressed to body of adminiculum (three plates in *incisa*, Fig. 47), forming dorsal lobes posterodorsally over median lobe (Figs 8). Additional pair of processes alongside dorsal spine in some species (Figs. 7, 8), elongate dorsal processes in *mitrata* and *anasazi* (Figs. 269, 284), wing-like expansions in *pellucida* (Figs. 196, 197). Median lobe small to large (one eighth to one half total height of adminiculum), pale with dark sclerotization along posterior margin, beak often present (Fig. 400); variously-placed dorsoventral carinae in most species (Figs. 8, 432). *Vesica and intromittent organ*: As in Figs. 9, 10. Intromittent organ of variable length, usually extending from vesica forward to abdominal segments 3–4 or even further before curving posteriorly. *Eighth sternum* (8S): Posterior (sclerotized) margin often shallowly concave (Fig. 240), strongly so in *eurystyla*, *melanderiana* (Fig. 67) and others, strongly biconcave in *sinistra* (Fig. 348). Posterior (membranous) apical margin with long yellowish setae (often reaching A9S) usually arranged in complete band (Fig. 421), but sometimes divided medially, as in *sinistra* species group (Fig. 350), or in paired patches of shorter setae in *incisa*, and *melanderiana* (Fig. 67). Most setae microscopically carinate (Figs. 98, 287), carinae corrugated to flat. Small lateral sclerites at ends of setal band, each bearing several elongate, sometimes coarse setae (Figs. 81, 113, 330). Usually a median membranous lobe in region between 8S and 9S (Fig. 241), varying in length from minute to over twice basal width, of variable shape (Figs. 82, 242, 267), but usually somewhat flattened and covered by microtrichia. *Ovipositor*: Length 10T + cerci/length 6T = 1.9–3.1 (mean = 2.4 ± 0.3); length 8S + hypogynial valves/length 6T = 1.5–3.2 (mean = 2.5 ± 0.4). Length 8T+cerci/length 8S + hypogynial valves = 1.0–1.7 (mean = 1.2 ± 0.2). *Terga 8–10*: Posterior border of *eighth tergum* often with broad median convexity. Ninth tergum with lateral area usually flat and smooth, rarely with faint lines, in *eurystyla* group with distinct tubercle (Fig. 102). Tenth tergum well sclerotized, setae in nearly all species pale and microscopic, with indistinct sockets (setae pale and lengthened, with large sockets in *eurystyla* group, Fig. 128); longitudinal apodeme complete extending length of tergum and well developed, in cases nearly reaching to 9T (Fig. 99) (incomplete in *incisa* (Fig. 56), usually

with a pale area bordering the darkened apodeme ventrally; posterior sclerotization of 10T forming border with short median "point" (Fig. 56). *Cerci*: well sclerotized, elongate, and tapering evenly to apices, often curved gently upwards subapically (Fig. 72), (in *eurystyla* group, cerci broadly expanded laterally with often irregular or toothed margin, Fig. 128). *Sternum 8*: With distinctive sclerotized pattern at base of hypogynial valves (and surrounding the 8S ridges extending anteriorly from base of hypogynial valves) (Fig. 40), in some species the pattern appearing granulate; ridges of 8S low to high (Figs. 271–276) (in *eurystyla* group vestigial (Fig. 129) to absent, with pale to dark coloration). *Hypogynial valves*: Dorsal border of hypogynial valves usually sinuous (Fig. 169, straight in *incisa* and *eurystyla* group), with distinct paler area at midlength (as viewed laterally). Apex of hypogynial blade rounded to nearly acute (Fig. 169), bifid in *eurystyla* (Fig. 102). *Sternum 9*: Ninth sternum present as fused valvulae dorsally and vaginal apodeme (= genital fork, furca); fused valvulae elongate, tapering to apex (Fig. 57), length generally reaching infraanal apical notch, in some species, with membranous areas at base produced laterally; vaginal apodeme Figs. 359–367. *Other structures*: Infraanal plate (10S) divided apically, with a few long setae, shorter thicker setae scattered (Fig. 118); spermathecae three in number, usually dark, with scales near base or extending along one side (scales absent in some species); cuticle smooth or reticulate.

The subgenus *Eremotipula* has been based on characters of the male hypopygium only (e.g., Alexander 1965, also see key in Alexander & Byers 1981), but characters of the female genitalia also allow placement of female specimens in this subgenus with confidence. There are combinations of non-genitalic features, however, that allow females of many species of *Eremotipula* to be distinguished in a preliminary sort from those of *Lunatipula* and related subgenera of *Tipula*. These characters are: femora with brown to dark brown, subapical transverse rings; wing vaguely patterned or clouded, with pale streaks in anal cell and band along cord and brown spots at end of Sc and origin of Rs; abdomen with dark brown sub-lateral patches, often contiguous and forming a complete line. Some species of western Nearctic *Triplictipula* also have femoral rings and brown spots over Sc and Rs, and could be confused with

species of *Eremotipula* based on non-genitalic features only.

Taxonomic History

C. R. Osten Sacken collected the first specimens of *Tipula* (*Eremotipula*) in 1876 (*sackeni* described in this revision), but it was not until 25 years later that R. W. Doane studied and described the first species in the group, *impudica*, *albocincta* (here regarded as synonym of *impudica*), *incisa*, and *clara*. Doane (1912) renamed the preoccupied *clara* as *pellucida* and described *flavicomma* (synonym of *incisa*) and *pyramis* (synonym of *pellucida*). C. P. Alexander added *kausensis* in 1918 (later to be regarded as a synonym of *incisa*). W. G. Dietz (1921) grouped the species (excepting *incisa* and synonyms) informally as the *Tipula impudica* group, and provided the first descriptions, keys, and illustrations of the characters of the group, particularly those of the male genitalia. In addition he described eight new species, *dimidiata*, *diversa*, *lyrifera*, *madina*, *mitrata*, *sinistra*, *spurnata* (here regarded as a synonym of *sinistra*), and *spaldingi*.

The next additions to the group appeared over twenty years after Dietz's revision, when Alexander (1942) described *eriensis* (here regarded as synonym of *incisa*). Several species or subspecies were described in the next six years by Alexander, including *carunculata* (here regarded as synonym of *lyrifera*) (1945b), *coconino* (here regarded as synonym of *dimidiata*), *kaibabensis*, and *incisa queres* (1946a), *macracantha* (1946b), *biproducta* and *spinirecta* (1947), *utahicola* and *woodi* (1948). Later, Alexander described *leiocantha* (1959) and *incisa picturata* and *kirkwoodi* (1961).

The *Tipula impudica* species group was formally designated by Alexander (1965a) as a new subgenus, *Tipula* (*Eremotipula*), with *impudica* as type species. Alexander offered a brief subgeneric description, described four Californian species (*helferi*, *melauderiana*, *middlekauffi*, and *schusteri*), and listed 20 additional species in the group. *Tipula incisa* and its synonyms (*flavicomma*, *kausensis*, and *eriensis*), and *T. kirkwoodi* and *spinirecta*, all remaining in *Lunatipula*, were not recognized as belonging to *Eremotipula* until this current revision.

In 1967, Alexander published the first key to any of the species of *Eremotipula* since that of Dietz (1921). Alexander's key included ten Californian or regional species with illustrations of the

taxonomically important parts of the male genitalia. The last species to be included in the group, previous to the eight new species described in this revision, was *eurystyla* (Alexander 1969). The species were cataloged by Theischinger & Theowald (1981). Teale (1984) reviewed the six species occurring in the southern Rocky Mountains, including a key and brief redescriptions. Gelhaus (1989) reviewed the group and provided a phylogenetic analysis of the species relationships based on male characters only; that work forms the core for what has been expanded on and published here. A checklist of the species of *Tipula* (*Eremotipula*) as currently recognized by this revision can be found starting on page 42.

Geographic Distribution

The subgenus *Eremotipula* is Nearctic in distribution (Fig. 43). One species, *incisa*, is widely distributed in central and western North America, occurring as far east as the Great Lakes region. All other species in the subgenus are found in an area generally bounded by the Rocky Mountains in the east and the Sierra Nevada in the west. A high percentage of these are concentrated in and around the Great Basin desert, particularly its eastern edge in Utah, and also in the Mojave Desert. Fewer species occur in the Sonoran Desert region and none in the Chihuahuan. The subgenus is mostly absent from the western flank of the Sierra Nevada, and entirely absent from the Central Valley of California and the Coast Ranges of the Pacific States (except the Transverse Ranges of southern California). Only one species, *sackeni*, enters Mexico (northern Baja California).

The species of the subgenus inhabit a range of elevations from less than 100 m to 3810 m.

Seasonal Distribution

Adults of *Eremotipula* can be found from late March to mid-August, with a few anomalous records from September and October (*incisa*, *impudica*, *kaibabensis*). Not surprisingly, the timing of emergence is strongly influenced by elevation and latitude, with an increase in either generally causing emergence later in the season. The earliest emergence occurs in the areas of low elevation in Arizona, southern California and eastern Washington, with the latest emergence at high elevations throughout the west (particularly the Sierra

Nevada of California and the Rocky Mountains in Colorado).

Habitat

Species of *Eremotipula* can be found in a wide variety of habitats in and surrounding the North American deserts, with some of the high elevation habitats decidedly unlike desert. Shrubby vegetation is common to most of these habitats, probably related to the occurrence of the immatures in the soil under shrubs. A few examples will illustrate this. *Tipula melanderiana* and *larreae* are both found in the extremely xeric desert at Deep Canyon, Riverside Co., California, where the vegetation is dominated by creosote bush (*Larrea divaricata*), brittle bush (*Eucelia farinosa*) and burro bush (*Ambrosia dumosa*). Both species also occur in the neighboring Santa Rosa Mountains, among single-needled pinyon pine (*Pinus monophylla*), juniper (*Juniperus californica*) and an understory of scrub live oak (*Quercus turbinella*), *Fallugia paradoxa* and buckwheat (*Erigeronum fasciculatum*) at Pinyon Flats, and in red shank and chamise (*Adenostoma* spp.) chaparral at a nearby site. Certainly, although the crane flies are common to all three sites, no one species of dominant shrub is. Thus, *larreae* and *melanderiana* are not dependent on any single species of shrub, although they do occur in xeric habitats dominated by shrubs.

Tipula sinistra occurs widely in western North America, generally at high elevations. Although it has been collected in spruce, fir and pine forests, these habitats nearly always have interspersed open areas of sagebrush (*Artemisia tridentata*). In Nevada, *sinistra* is found in high elevation steppe of sagebrush and antelope brush (*Purshia tridentata*) without trees.

This dependence on shrub-dominated vegetation by most species of *Eremotipula* does not apply to *incisa*. This sister species of the remaining species of *Eremotipula* is found in riparian woodlands lacking a dominant understory of aridland shrubs, to judge from the few records available from the Great Plains, including reared immatures. Whether *incisa* is also restricted to riparian habitats in western North America is unknown; there are few habitat records for this species from western localities.

No species have been collected from grassland devoid of a shrub element, and there are few

records of species occurring in closed canopy forest without areas of shrubs (see *byersi* and *lyrifera*).

Natural History

There have been no studies of the biology of any species of *Eremotipula*. Previous published information consisted only of brief comments on the habitats of a few species. This section is also based on scanty information, derived from scattered field observations. The few conclusions here can serve only as indications for future studies.

Adults. The adult is the most conspicuous, easily observed and collected stage of *Eremotipula*, but it is also the most ephemeral. Adults in the laboratory live only two to seven days after eclosion, with most surviving three to four days. Survival in a natural setting might be even shorter, considering effects of climate and predators on mortality for tipulids in general (Pritchard, 1983). Adults were not seen to feed.

I observed little diurnal activity of adults, possibly because of the hot, windy conditions often present in the exposed habitats of these flies. Adults rest in trees, if available, (generally juniper or pinyon pine), often flying to the tree and moving deeper into the shaded vegetation before settling. The flies can be detected as they reposition themselves when the branches are moved by wind, but otherwise their yellowish-brown body coloration is difficult to see in these situations. Teneral flies were usually found in lower shrubs and not in trees.

Males are swift fliers relative to those of many other species of *Tipula*, and may fly 10–15 meters or more before alighting, particularly when aided by wind. Females of some species (*helferi*, *anasazi*) appear to be poor fliers when fully gravid, but those of other species (particularly the *diversa* group) readily take flight. Often the distribution of adults was clumped. For example, in Beaver Co., Utah, adults of *lyrifera* were abundant in several neighboring juniper trees (15+ adults per tree) but few were found in trees away from this area. I could see no differences to account for this concentration. At Timber Creek, Nevada, I found various species concentrated in clumps of nettle along the stream, possibly due to the higher humidity there.

I observed increased activity of males late in the afternoon preceding or directly after sunset.

For example, in Washington Co., Utah, I noted males of *madina* making straight-line flights between trees and shrubs in the late afternoon (around 6:00PM, sunset about 8:30PM), whereas little of this activity was observed earlier in the afternoon. Males of several species were observed presumably searching for females among trees or tall shrubs. This activity consisted of the male flying in a bouncing fashion along a branch to its apex, then moving over or up to a new branch, and continuing its bouncing flight; this is reported for other Tipulinae as well (Pritchard 1983). This activity appears to continue well into darkness, as I observed males "searching" up until I could not see anymore. Males were attracted to UV and white lights long into the night if temperatures were favorable. In chaparral, where shrubs form large, connected stands, males of *melanderiana* were observed to make long, fast, high flights over the vegetation, dropping down and disappearing within the shrubs, with no males seen searching the terminal branches.

Although copulation was observed several times in the laboratory among reared adults, I saw it only once in a natural setting. At Angel Creek, Nevada, I found two pairs of *sinistra* in copula at 3:45 and 4:10 PM (PDST). That these flies were mating in the afternoon, although male activity was seen most often in the evening in other species, is probably related to the occurrence of *sinistra* in high elevation habitats which get too cold for activity at night. Females were observed ovipositing in the laboratory, but oviposition was not seen in the field.

Immatures. Although the immatures represent a much longer part of the life cycle than do the adults, they occur in the soil, which prevents easy observation and collection. I found that eggs do not hatch promptly after laying and probably are in a state of diapause as reported for a grassland species of *Tipula* (*Triplicitipula*) (Hartman & Hynes 1980) and observed in species of the subgenus *Lunatipula* in Kansas (pers. obs.). The immatures were largely unknown prior to this study, but I reared and associated larvae and pupae for *anasazi*, *dimidiata* and *diversa* and pupae only for *kaibabensis*, *lyrifera* and *sinistra*. The immatures of *incisa* have been reared previously but not described (G. W. Byers, pers. comm.). The immatures will be treated in a separate paper but will key to *Lunatipula* in Gelhaus (1986).

All larvae were found in the soil under shrubs of sagebrush (*Artemisia tridentata*), cliff rose (*Cowania mexicana*) and rabbitbrush (*Chrysothamnus* sp.). Details can be found in the "habitat" section under the individual species. Larvae occurred shallowly in the usually damp soil, as has been noted elsewhere for terrestrial *Tipula* in general (Gelhaus 1986). Larvae feed on the detritus that accumulates under the shrubs, usually leaves and twigs from the shrub, along with dead parts of herbaceous plants. The litter layer is usually

sparse, often only a centimeter thick. None of the species of the low- elevation deserts has been reared. The larva of *incisa* occurred in riparian woodlands, not arid shrubland, and fed upon leaf litter of largely cottonwood trees (*Populus deltoides*) (G. W. Byers, pers. comm.).

Pupation takes place one to two weeks prior to adult emergence, with the pupae occurring in the habitat of the larvae, but often slightly deeper in the soil. Pupae move to the soil surface prior to eclosion.

KEY TO MALES OF *TIPULA* (*EREMOTIPULA*)*¹

1. Membranous apex of eighth sternum with flat, linguiform process, fringed with setae (Fig. 201); a slightly darkened, acuminate, elongate lobe, between 8S process and 9S (Fig. 199), extending between A9S to base of adminiculum *pellucida*
 Membranous apex of 8S usually concave or straight (Fig. 240), rarely with short process (*eurystyla*, *schusteri*, Fig. 182); membranous lobe between 8S and 9S not reaching A9S and adminicular base (Figs. 2, 427), or lobe absent 2
- 2(1). Dorsolateral margin of BS with large flattened lobe, equal in height to outer basal lobe of ID (Fig. 44); ventral lobe of A9S with numerous, elongate twisted setae; western to central North America *incisa*
 Dorsolateral margin of BS not with large flat lobe (Figs. 2, 225, 427); ventral lobe of A9S with short, straight, often thickened setae (Figs. 189, 342); western North America only 3
- 3(2). Dorsolateral margin of BS produced into a broad, flat spine, with distinct to indistinct posterior depression (Figs. 94, 145); ID without crest (small crest in *maderensis*) (Figs. 109, 90) 4
 Dorsolateral margin of BS not produced into a broad flat spine, although an elongate short, inwardly-curved spine may be present (Figs. 219, 427), posterior depression absent; ID with crest (Figs. 5, 64) 11
- 4(3). STP membranous or minute, ventral plate shelf and its lobe lacking (Figs. 120, 121); (*eurystyla* group) .. 5
 STP not minute, easily visible, 9T with ventral lobes and shelf, (Figs. 54, 234–235) 6
- 5(4). 9T appearing to lack dorsal lobes and STP (Figs. 120); ID with characteristically shaped OBL with narrowed apex, extensively fused with anterior half (Fig. 122); eastern Sierra Nevada, California .. *helferi*
 9T with STP a small membranous, haired lobe and short dorsal lobes (Figs. 132); OBL distinct from rest of dististyle, with broad, rounded apex (Fig. 135); foothills surrounding southern Central Valley of California *spinirecta*
- 6(4). Wing with conspicuous, longitudinal white streaks along cells *m* and *r*₅, and along cell *cu* and anal cells; OBL an elongate, dorsoposteriorly directed blade (Figs. 144, 159) 7
 Wing lacking the longitudinal white streaks; OBL variable, usually not an elongate blade (Figs. 163), if so then directed posteriorly (Fig. 381) 9
- 7(6). Apical half of basistylar lobe abruptly narrowed into a strong dorsal spine (Fig. 154); ID with a small crest (Fig. 159) *maderensis*
 Apical half of basistyle broader (Fig. 148); ID crest absent (Fig. 151) 8
- 8(7). 9T with distinct dorsal lobes, compressed STP and irregularly shaped ventral lobes (Figs. 152–153), known from Santa Cruz Co., Arizona *rogersi*
 9T with indistinct dorsal lobes, depressed STP and flat truncate ventral lobes (Figs. 140, 142); known from Santa Rita Mountains, Arizona *kirkwoodi*
- 9(6). STP elongate, with upturned, pale apex (Fig. 88); OD large, club-shaped, as high as ID (Fig. 91) *eurystyla*
 STP short, depressed and dark (Figs. 105, 115); OD small, not reaching lower beak of ID, with short anterior extension (Figs. 104, 114) 10
- 10(9). Wing faintly patterned with brown; 8S with straight membranous apical margin (Fig. 113), Utah *utahicola*

¹The species *elverae* is not keyed here as the male is unknown.

- Wing strongly patterned with brown coloration; 8S with apical membranous margin convex medially (Fig. 116), eastern Sierra Nevada, California *baumanni*
- 11(3). Apex of outer basal lobe of ID broad, scarcely narrowed from width at base (Figs. 64, 76, 164); ventral lobes of 9T elongate and rod-like (Fig. 75) 12
- Apex of outer basal lobe of ID narrower than base, sometimes strongly so (Figs. 227, 303, 344, 387); ventral lobes of 9T variable but usually not rod-like (Figs. 177, 299, 340, 416; exception: *spinosa* (Fig. 317) which has the OBL narrowed apically) 14
- 12(11). Dorsal lobes of 9T attenuate, exceeding STP in length (Fig. 160) *macracantha*
- Dorsal lobes extremely short, not exceeding STP in length (Figs. 60, 74) 13
- 13(12). Dorsal lobes of 9T divergent, with subacute apices (Fig. 60); midventral region of 9S with membranous, haired protuberance (Fig. 68); thorax and hypopygium dark reddish brown, wings light grayish brown *melanderiana*
- Dorsal lobes of 9T broadly rounded (Fig. 74); midventral region of 9S smooth and bare; thorax and hypopygium brownish gray; wings light brown *larreae*
- 14(11). BS with large horn-like lobe arising dorsal to A9S near ventral basistylar suture (Figs. 309–310), lobe subequal to outer basal lobe in length *biproducta*
- BS with projections much smaller and opposite posterior condyle of ID, only typical lobe near basistylar suture (Fig. 2) 15
- 15(14). OBL nearly smooth laterally and broad (Figs. 217, 103); crest well-developed along upper beak (not in *jicarilla*) with groove between crest and lateral surface of beak 16
- OBL somewhat excavated laterally, usually with longitudinal ridge, (Figs. 303, 319); crest not well developed anteriorly with, at most, narrow groove between crest and body of upper beak 20
- 16(15). Ventral lobe of A9S protruded and large, nearly equal to the dorsal lobe in size (Figs. 216, 225) 17
- Ventral lobe of A9S partially concealed and small, less than one quarter the size of the dorsal lobe (as in Fig. 427) 18
- 17(16). Dorsal lobes of 9T usually with a truncate apex, sometimes shortened with pointed apex (Figs. 234, 236–238); dorsal lobes of adminiculum with several dorsal teeth (Fig. 229); setal band of eighth sternum with uniformly slender setae (Fig. 240); New Mexico to British Columbia *impudica*
- Dorsal lobes of 9T slender, apices subacute (Fig. 214); dorsal lobes of adminiculum with bifurcate posterior spines (Fig. 220), setal band of 8S with single line of thicker setae and medial patch of fine setae (Fig. 223); northern Arizona and southern Utah *byersi*
- 18(16). OBL of ID with apex narrowed (Figs. 258) 19
- OBL with broad, nearly truncate apex (Fig. 250) *madina*
- 19(18). Dorsolateral margin of BS with short, curved spine (Fig. 257); OBL with a protuberance anteriorly (Fig. 258); 9T with well developed ventral lobe (Fig. 256); median lobe of adminiculum greatly expanded laterally, deltoid with serrate margins in posterior view (Fig. 261); northern Great Basin and adjacent area *spaldingi*
- Dorsolateral margin of BS with slight, rounded lobe only (Fig. 205); OBL without protuberance (Fig. 210); 9T with ventral lobe not developed (Fig. 207); median lobe of adminiculum small, not expanded (Fig. 208), New Mexico *jicarilla*
- 20(15). Apical membranous margin of 8S produced into short, rounded medial lobe (Fig. 176); outer basal lobe of ID small and strongly curved laterally, apex subacute (Fig. 179) *schusteri*
- Apical membranous margin of 8S not produced (Figs. 421); outer basal lobe of ID shaped otherwise (Figs. 303, 327, 431) 21
- 21(20). Outer basal lobe of ID elongate, $L/W > 2.5$ (Figs. 371, 381) 22
- Outer basal lobe of ID shorter, $L/W < 2.5$ (Figs. 319, 334) 27
- 22(21). Dorsolateral margin of BS (opposite posterior condyle) with one large, inwardly-curved spine (two in *lyrifer*) (Fig. 427); OD with moderate to long anterior extension (Figs. 424–425); thoracic setae short and dark 23
- Dorsolateral margin of BS broadly produced, but not spine-like; OD without an anterior extension; thoracic setae long, and light brown; northern Arizona *dissipina*
- 23(22). Dorsal lobes of 9T with strongly toothed apical margin (Fig. 395); dorsolateral margin of BS with two closely-set spines *lyrifer*
- Dorsal lobes of 9T with nearly smooth or minutely-toothed margin (Figs. 378, 415); dorsolateral margin of BS with large, single, inward-curved spine 24
- 24(23). Posterior margin of ID (dorsal to posterior condyle) strongly convex (Figs. 5, 431); ventral lobe of A9S

- with numerous, thick, short, reddish brown setae (Fig. 429); outer basal lobe of ID bent or twisted along length25
- Posterior margin of ID either concave or weakly convex (Figs. 381, 387); ventral lobe of A9S with pale setae not strongly thickened, some long (Figs. 380, 386); outer basal lobe of ID straight26
- 25(24). Outer basal lobe of ID with prominent, well-developed ridge, distal blade bent twice along length (Figs. 4, 6), apex not twisted*sackeni*
- Outer basal lobe of ID with weakly developed ridge, blade straight distally, apex of lobe twisted (Fig. 431)*diversa*
- 26(24). Outer basal lobe of ID with well developed, shelf-like ridge (Fig. 381); Utah northern Arizona, southern Nevada*evalymae*
- Outer basal lobe of ID with ridge low and weakly developed (Fig. 387); eastern California to central Nevada*leiocantha*
- 27(21). Outer basal lobe of ID extended and narrowed distally, with digitiform apex (Fig. 319); membranous lobe of 8S elongate and slightly darkened (Fig. 2); ventral lobes of 9T rod-like (Fig. 317)*spinosa*
- Outer basal lobe of ID with apex broadly rounded (Figs. 303, 336) or narrowly truncate (Fig. 344); membranous lobe of 8S, if large, not darkened (Figs. 265, 330); ventral lobes of 9T short (Figs. 299, 333)28
- 28(27). Membranous lobe of 8S easily visible, yellowish, broad, and thick (Figs. 330, 350); ventral lobes of 9T thickened, apex truncate or pointed (Figs. 325, 340)29
- Membranous lobe of 8S (if visible) flat, narrow and pale (Figs. 265, 306); ventral lobes of 9T short, flat and rounded (Figs. 264, 299)31
- 29(28). Wing with Cu and m-cu seamed with light brown, a pale band along cord (Fig. 446); legs brown with yellowish subapical ring; male hypopygium usually bent upward at nearly right angle to rest of abdomen; ventral lobe of A9S with short, thickened, reddish brown setae30
- Wing nearly unicolorous, light grayish brown without pale band along cord; legs yellowish brown with indistinct brown femoral rings; hypopygium not strongly bent upward; ventral lobe of A9S with long slender setae that are directed ventrad (Fig. 326)*woodi*
- 30(29). Outer basal lobe of ID with sharply defined ridge with setae, apex of lobe narrowly subtruncate (Figs. 344–345); membranous lobe of 8S short, broad and distinctly pyramidal (Fig. 350)*sinistra*
- Outer basal lobe of ID with indistinct ridge not associated with setae, apex of lobe rounded (Fig. 336); membranous lobe of 8S linguiform (Fig. 338)*middlekauffi*
- 31(28). Ventral lobe of A9S with 1–2 black, spiniform setae (Fig. 282)*mitrata*
- Ventral lobe of A9S without black, spiniform setae32
- 32(31). Dorsal lobes of 9T widely divergent, broad basally (Figs. 170, 263)33
- Dorsal lobes of 9T weakly divergent, elongate, and narrow (Figs. 288, 298)34
- 33(32). Ventral lobe of A9S with numerous, thickened, short, laterally-directed setae; membranous lobe of 8S minute, not visible outwardly (Fig. 175); eastern Oregon to Nevada*artemisiae*
- Ventral lobe of A9S with long, slender setae (Fig. 268); membranous lobe of 8S long and easily visible outwardly, about one third to one half length of apical setae on 8S (Fig. 265); northern New Mexico*anasazi*
- 34(32). Membranous lobe of 8S pale and elongate, nearly equal to length of apical setae (Fig. 306); outer basal lobe of ID with strong ventral ridge on lateral surface (Fig. 303); northern Arizona, Utah, and Colorado*kaibabensis*
- Membranous lobe of 8S minute and concealed (Fig. 295); outer basal lobe of ID with isolated, low ridges (Fig. 292); west central Arizona to southern New Mexico*dimidiata*

The following identification key to females of the species of *Tipula* (*Eremotipula*) must be considered very preliminary. Of the 35 species known from males, I have females associated for only 23; remaining unknown are *baumanni*, *kirkwoodi*, *maderensis*, *rogersi*, *spinirecta*, *utahicola* (all *enrystyla* group); *biprodacta*, *spinosa* (*biprodacta* group); *byersi* (*iupudica* group); *dissipina* (*diversa* group); *middlekauffi* (*sinistra* group); and *schusteri*

(unplaced group). An additional species, *elverae*, is known from the female only. Of the species with known females, many of these are known from few specimens (e.g., *artemisiae*, *woodi*) and therefore species variability in terms of female morphology has been difficult to assess.

There are no keys to distinguish females of the subgenera of *Tipula* in North America, particularly those subgenera of the *Lunatipula* group. Females

of *Eremotipula* can be generally preliminarily sorted from other female *Tipula* by body and wing coloration such as pale streaking of the wing posteriorly; wing variegated with light brown; femora with dark brown subapical rings; abdomen with at least lateral and often dorsal dark longitudinal lines (details given in subgeneric description). Synapomorphies of most species include these characters of the female genitalia sometimes observed without clearing: complete well-developed longitudinal apodeme of 10T (except *incisa* where it is only along posterior half); sclerotization on the floor of 8S divided and restricted to median and lateral pairs of lines (except *eurystyla*); slight to well developed pair of ridges on upper surface of 8S extending forward from base of hypogynial valves (vestigial in *pellucida*, *helferi*, *eurystyla*); dorsal border of hypogynial valve blades sinuous (not in *incisa*, *eurystyla*, *helferi*); medial area of hypogynial valves (as viewed laterally) paler than surrounding area (not *eurystyla*, *helferi*, *incisa*) and possibly spermathecae with scales present near base (*incisa*, *melanderiana*, *larreae*), or extending along one side only; (scales absent in *eurystyla*, *helferi*, *pellucida*, *sinistra*).

I have included as many features as possible

that are readily observable, e.g., wing or thoracic coloration, but these features often exhibit subtle differences, and need to be used carefully. Confirmation usually requires observation of the internal features of the female genitalia. Because of the importance of the inner ridge of the 8S for identification of females, and the difficulty in observing this in dried specimens, clearing of the genitalia may be necessary for accurate identification. Preservation in alcohol, or spreading of the cerci and hypogynial valves soon after collection (for specimens to be dried, Fig. 1) will facilitate observation without further preparation.

As can be seen in the section on sympatry, numerous species of *Eremotipula* can be found at the same locality at the same time. I have followed these guidelines in determining females to species based on the male stage: specimens collected *in copula* (this must be noted on the label and not simply be two individuals on the same pin), repeated association of a female morphotype with similar males of one species, and close similarity of wing and body coloration in males and females (but note that a slight dimorphism occurs in wing pattern in some species). None of these can be considered absolute evidence.

KEY TO FEMALES OF *TIPULA* (*EREMOTIPULA*)

1. Lateral edges of ninth tergum each with a well developed tubercle (Figs. 99, 102, 128); hypogynial valves vestigial, not bladelike (Figs. 102, 199, 127); cerci expanded laterally, edge irregular (Figs. 99, 128); setae on 10T moderate to long, with enlarged, bubble-like sockets (Fig. 128) (*eurystyla* group, females of six of the nine species in this group are unknown) 2
- Lateral edges of ninth tergum without tubercle (Fig. 56); hypogynial valves elongate usually, always bladelike (Figs. 37–39, 55), cerci compressed, lateral surface not greatly expanded, edge straight (Figs. 56, 410–412); 10T with microscopic pale setae, sockets indistinct (most outgroups, all other *Eremotipula*) 4
- 2(1). Apex of hypogynial valve unequally bifid (Fig. 102); Utah *eurystyla*
- Apex of hypogynial valve rounded (Fig. 127); Utah and California 3
- 3(2). Lateral border of 8S with well-developed, outwardly projecting, lateral flange (Fig. 130); California *helferi*
- Lateral border of 8S without lateral flange (Fig. 118), Utah *elverae*
- 4(1). Floor of 8S with pair of longitudinal ridges bordered by 2 pairs of pigmented lines (i.e., lateral and medial to ridges) (Fig. 40), remainder of floor of 8S pale (all other *Eremotipula*) 5
- Floor of 8S without distinct ridges and pigmented lines (Figs. 41, 42) other *Tipula*
- 5(4). Hypogynial valve blade with sinuous border, distinctly pale medially (Fig. 71); tenth tergum with complete longitudinal apodeme (as in Fig. 99) 6
- Hypogynial valve blade with straight dorsal margin, evenly colored (Figs. 55, 58); tenth tergum with apodeme ending at midlength (Fig. 56) *incisa*
- 6(5). Hypogynial valve blade shortened, apical half abruptly narrowed (Fig. 409); cerci broad dorsally (Fig. 413) *lyrifera*
- Hypogynial valve with apical half not so strongly reduced in width (Fig. 408); cerci slender dorsally (Fig. 412) 7

- 7(6). Wings with brown seam along Cu and m-cu veins (Fig. 446); several setae along posterior margin of tergum 1 light brown and elongate (4–6x as long as other dark setae, Fig. 343); 8S ridges elongate, broad medially and lightly pigmented (Figs. 352, 354–358) *sinistra*
[The as yet undiscovered female of *middlekauffi* will probably key here; northeastern California]
- Without combination of wing pattern, elongate setae and ridges 8
- 8(7). Wing mostly unicolorous light gray or brown, with costal and subcostal cells deeply yellowed and contrasted with rest of wing (Fig. 443); white band along cord (faintly so in *pellucida*, distinct in *jicarilla*) but with no other streaking 9
- Wing without strongly yellowed costal and subcostal cells, pale streak around stigma and along cord, often with additional streaks in medial and anal cells (Figs. 444, 454, 455); if costal cell strongly yellowed (*impudica*) then pale streak along veins A₁ 11
- 9(8). Membrane adjacent to anterior end of ridge of 8S expanded into lobe (Fig. 202), inner pair of pigmentation stripes of 8S mostly confluent (Fig. 203), thorax mostly brownish gray, abdomen with three dark stripes, lateral pair grayish; wing with band at cord scarcely evident (Fig. 443) *pellucida*
- Membrane not produced; pigmentation stripes not confluent, body coloration variable, but usually not extensively brownish gray; pale band at cord either distinct or absent 10
- 10(9). Wing without pale band at cord; hypogynial valve broadest basally; 8S ridges as in Fig. 353, northern Utah and eastern Nevada *woodi*
[The as-yet-discovered female of *disspina* may key here; northern Arizona]
- Wing with distinct pale band along cord; hypogynial valve not noticeably broadest at base (Fig. 213); ridges of 8S (Figs. 212–213), central New Mexico *jicarilla*
- 11(8). Small dark spot at junction of Sc and R₁, and at origin of Rs (Fig. 456); thoracic dorsal stripes dark brown and distinct 12
- At most, spot at junction of Sc and R₁; thoracic stripes variable, often scarcely darker than surrounding color 14
- 12(11). Body coloration dark reddish brown, pale streak along vein M in addition to band along cord; ridges of 8S darkly pigmented (Figs. 71, 72); southern California only *melanderiana*
- Body coloration not distinctly reddish brown, more yellowish or dark brown; wing with large pale patch extending from cell *m* to A₁, with pale streak at base of A₁, dark seam around m-cu and Cu to wing margin (Fig. 456); ridges of 8S pale and elongate (Fig. 407); widespread distribution including southern California 13
- 13(12). 8S with broad lateral groove, extending nearly to hypogynial valve (best viewed in dried, unprepared specimen) (Fig. 406); southern California to New Mexico, north to southeastern Wyoming ... *diversa*
- 8S with narrow lateral groove, ending far from base of hypogynial valves (Fig. 405); Pacific Coast ranges to southern British Columbia east to northeastern Wyoming *sackeni*
- 14(11). Wing overall light brown, patterned with pale area in cell *r*₅ (contrasting with brown isolated area distally in cells *r*₁₊₂ and *r*₃), along with paler bands along cord and streaks along vein A₁ and in cell *a*₁ (Fig. 455); abdomen bright yellowish-brown with nearly continuous dark medial line; each internal ridge of 8S dark, with accessory dark ridge laterally, a shallow cavity formed in-between (Figs. 168, 169), southern deserts *macracantha*
- Wing usually without contrasting pale area in cell *r*₅ although other paler areas may be present (Fig. 454); abdomen not usually bright yellowish brown, dark lines variable; 8S without accessory ridges, pigmentation of internal ridges variable 15
- 15(14). Wing with brown spot at junction of veins Sc and R₁ (may be pale); each inner ridge of 8S scarcely broadened beyond attachment to hypogynial valve, dark anteriorly, usually pale posteriorly (Figs. 69, 70); southern California *larreae*
[The as yet undiscovered females of *biproducta*, *schusteri* and *spinosa* may key here due to wing patterning; all southern California]
- Without the combination of wing coloration, ridge morphology and coloration and geographic distribution 16
- 16(15). Wing nearly always with three contiguous pale areas extending from near base of cell *m* to along vein A₁ (appearing as large contrasting pale spot) (Fig. 454); female abdomen usually bright yellowish brown with dorsal dark markings not contiguous as line but reduced as isolated spots; each 8S ridge only moderately developed; brown pigmentation laterally but pale dorsally (Figs. 275, 276); Arizona and New Mexico *mitrata*

[*kaibabensis* has a similar wing pattern, but ridge greatly developed—see couplet 20; the female of *byersi* is unknown but may key here; northern Arizona and southern Utah]

- Wing usually without a large pale area extending from cell *m* to vein *A*₁ (Fig. 447, but see *kaibabensis*, Figs. 451, 453); coloration and ridge development variable; widespread17
- 17(16). Each 8S ridge well developed and pale overall, with broadest portion at or near midlength, giving an elongate appearance (Fig. 408), ridge length 1.1–1.3 mm18
- 8S ridges variable, but broadest usually posteriorly, not at midlength, often darkly pigmented but may be pale throughout, ridge length maximum 1.2 mm but usually less than 1.0 mm19
- 18(17). Apex of hypogynial valves usually subacute (Fig. 408); Utah, northern Arizona to southern Nevada (Spring Mountains) *evalyinae*
- Apex of hypogynial valves more rounded; California (Sierra Nevada, White Mountains) to central Nevada *leiocantha*
- 19(17). Ridges of 8S abruptly broadened posteriorly, preceding base of hypogynial valves (Figs. 274, 278), ridge often heavily pigmented laterally (less so in *spaldingi*)20
- Ridges of 8S without abrupt broadening posteriorly, ridge only moderately broad at most, and each end with gradual narrowing (Figs. 244, 271); ridge usually with little or no pigmentation23
- 20(19). Wing usually with broad pale spot extending from base of cell *a*₁ to *m* (Figs. 451–453); inner ridge of 8S usually erect in dried specimens, usually completely dark laterally (may be lighter) (Fig. 274); Utah, northern Arizona and southwestern Colorado *kaibabensis*
- Wing with at most pale streaks, particularly along vein *A*₁ and in cell *a*₁ (Fig. 447); ridge of 8S usually not erect in dried specimens (appressed to floor of 8S), with pigmentation otherwise (Fig. 278)21
- 21(20). Ridge of 8S brown laterally with pale dorsal border (Figs. 273, 278); wings with pale streaks posteriorly along vein *Cu* and crossvein *m-cu* in addition to those in cell *a*₁ (Fig. 447); central New Mexico *anasazi*
- Ridge of 8S usually only lightly pigmented; wing pattern otherwise22
- 22(21). Wing extensively patterned with pale and brown areas, including cell *R*₅ mostly pale, and brown areas isolated in cells *m*₁–*m*₄ and *a*₁, in addition to streak along cord; ridge of 8S (Fig. 244) northern Great Basin *spaldingi*
- [compare also with *madina* and *impudica*]
- Wing with pale streaks along cord and along vein *A*₁ and in cell *a*₁ (Fig. 448); ridge of 8S (Figs. 272, 277) Arizona, New Mexico and southwestern Utah *dimidiata*
- 23(19). Wing with cells *c* and *sc* usually strongly yellowed, contrasting with adjacent coloring of cell *r*; wing with conspicuous pale streak along middle section of vein *A*₁ and in cell *m*₄; New Mexico to Wyoming westward to Oregon, Washington and southern British Columbia *impudica*
- Wing with cells *c* and *sc* light yellow, similar in coloration to that in cell *r*, not distinctly yellowed; wing with or without pale streaking along vein *A*₁, if present, then indistinct; Oregon and Nevada to central Utah24
- 24(23). Small species (body 17–18 mm, wing 12–14 mm long); wing without pale streaking along vein *A*₁; south-eastern Oregon to northwestern Nevada *artemisiae*
- Larger species (body 19–24 mm; wing 14–19 mm long); wing with pale streak along middle section of vein *A*₁; Central Utah to eastern Nevada *madina*

SPECIES TREATMENTS

Species Unplaced to Species Group

Tipula (Eremotipula) incisa Doane

Tipula incisa Doane 1901: 118; Alexander 1949: 284, loc.; Byers 1976: 22, discussion of types; Teale 1984: 57–58, loc., redesc., key.

Tipula flavicomma Doane 1912: 57; Byers 1976: 19–20, figs. 56–58 (hypo., lat.; ID, 9T), discussion of type.

Tipula kansensis Alexander 1918: 411–412; Rogers 1931: 337, loc.; Alexander 1946a: 503, subspp. status.

Tipula (Lunatipula) eriensis Alexander 1942: 285–286, fig. 31-P (9T); Alexander 1946a: 503, subspp. status.

Tipula (L.) incisa queres Alexander 1946a: 502–504, fig. 5 (hypo., lat.; 9T, vent.; ID, OD, 8S).

Tipula (L.) incisa picturata Alexander 1961: 84.

Diagnosis.—*Male*: Ninth tergum with short, dark, broad STP, dorsal lobes scarcely produced (Fig. 49); dorsolateral margin of BS with enormous, flattened lobe, equal in height to flat, elongate outer basal lobe of ID (Fig. 44); A9S with each dorsal lobe unequally divided, mesal portion large and swollen and ventral lobe small, circular

and entirely sclerotized, with numerous, twisted, elongate setae (Fig. 44); apex of 8S with several, thickened, lateral setae, each seta curved toward midline; two patches of denser, shorter setae on either side of midline. *Female*: Longitudinal apodeme of tenth tergum only half length (Fig. 56); dorsal margin of hypogynial valves straight, not sinuous (Fig. 58).

Description.—*Length*: Male 14–19 mm, female 21–26 mm. *Head*: Vertex and postgena yellowish brown to dark brownish gray, pruinose; where vertex dark, a pair of yellowish sublateral patches on occiput. Antennal length: male 4–5 mm. *Thorax*: Usually brownish gray in specimens from western North America, chestnut brown merging to gray posteriorly in specimens from Kansas and Oklahoma. Presutural scutum with five, dark brown to chestnut brown, longitudinal stripes, often only evident anteriorly or interrupted at midlength. Pleura usually brownish gray, darkest in some western specimens. *Legs*: Yellowish brown in all specimens. Femoral rings ranging from dark to light, to completely absent. *Wing*: (Figs. 438–441). Male 14–17 mm long, 3–4 mm wide, female 15–18 mm long. Costal and subcostal cells strongly yellowed. Stigma brown and distinct to light yellow and not distinguishable. Wing overall light brown or light brownish gray, with pale band extending along cord into discal cell, band sometimes narrow and indistinct. Contrast between light brown and pale areas most developed in specimens from western North America, a large brown spot at origin of Rs, a less distinct one at end of Sc, and a dark brown spot at base of cell *cu* and just before midlength, distal dark spot of *cu* preceded and followed by two large pale spots; pale band at cord extending along vein *M*₁, *M* and around stigma, reaching discal cell. In most specimens from Kansas and Oklahoma, one spot distinct near midlength of cell *cu* and one at origin of Rs, pale areas restricted to cord. Some Kansas specimens with only small spot at origin of Rs, with both stigma and pale band along cord obsolete. *Abdomen*: Terga 2–7 with sublateral and dorsal dark brown spots, usually spots nearly contiguous along abdomen, forming three stripes, dorsal markings sometimes indistinct. Edge of each tergum grayish, contrasting with dark spots. Marginal setae on tergum I elongate, yellowish, 4x as long as preceding setae. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/9S = 0.5. Dorsal lobes low, broad, about twice as wide as long (Fig. 49),

apex variable, slightly emarginate or subtruncate, or lateral corner produced and mesal corner reduced (Figs. 49–53). STP short, ratio of length STP/9T = 0.1–0.2, with slight dorsal ridge; process uniformly darkly sclerotized with smooth dorsal margin, with median ventral longitudinal invagination, scattered microtrichia dorsally near base, narrowing apically, with slight to well-developed medial apical notch. Cuticle of STP reticulate, without microtrichia. Ventral plate shelf rectangular anteriorly, abruptly narrowed in posterior half, with posterior corner produced into short lobe (Fig. 54). *Ninth sternum* (+ *basistyle*): Most of dorsolateral margin of BS produced into broad, flat, nearly rounded lobe (Fig. 44), about as high as outer basal lobe of ID (in dried specimens). A9S (Fig. 44) with dorsal lobes unequally divided into large, tumid, medial swelling and much smaller lateral one, both with numerous long, straight, yellowish setae, those on lateral swelling slightly longer and stouter. Ventral lobe of A9S small, rounded, completely sclerotized, distinctly separated from dorsal lobe, with long, yellow setae; apical third of each seta twisted. Ventral region of sternum membranous as in other species in subgenus, except extending laterally below base of adminiculum. *Outer dististyle*: A small, narrow blade (Fig. 46) usually scarcely expanded beyond basal width. *Inner dististyle*: Base broad, condyles scarcely distinguishable. Ventral surface of upper beak with strong ridges, lower beak smooth, rounded, elongate and curved strongly laterad. Entire upper beak expanded and shifted vertically upward with respect to base. Crest broad, rounded, short, with narrow gap between crest and beak, crest lightly sclerotized, with many crisscrossing striae and microscopic serrulations along dorsal margin; close-set, dark tubercles basally and extending along lateral surface of body of beak. OBL an elongate flat blade of nearly uniform width throughout (Fig. 45), L/W = 2.0–2.7, directed dorsally, with apical half slightly bent laterad. *Adminiculum*: Base lacking firm connection to A9S seen in other species of *Eremotipula*. Feet of adminiculum flat, wide, curved posteriorly, unlike other *Eremotipula*. Adminiculum beyond base of nearly uniform width, scarcely bent posteriorly, with three lateral overlapping plates (Figs. 47, 48) most posterior plate appressed to median lobe and with small acute point dorsally. Median lobe small, rounded; a pair of ridges on either side of adminiculum below median lobe.

Eighth sternum: Posterior (sclerotized) margin only slightly concave (although dark setae are often absent from a large median portion, giving impression of deep emargination). Membranous apical region with two low, broad protuberances covered with short, dense, yellow setae, setae increasing in length toward mid-line. Sclerotized lateral knob, with 3–5 thickened, smooth, elongate setae, curved toward midline, about twice as long as next longest setae on sclerite (Fig. 44); remaining setae on sclerite numerous, some smooth. All other lateral and medial setae with conspicuously broad carinae with wavy margins. Membranous region without lobe; a sclerotized line connecting lateral sclerites and extending behind setal patches. *Ovipositor:* Posterior border of eighth tergum slightly convex at midlength (Fig. 56). Lateral area of ninth tergum with fine lines, often area slightly swollen. Longitudinal apodeme of 10T extends only along posterior half, poorly sclerotized and strongly narrowed anteriorly (Fig. 56). Dorsal border of cerci nearly straight; each apex narrowly subtruncate and slightly swollen (giving a "knobby" appearance when viewed laterally, Fig. 55). Shallow, longitudinal groove extending along dorsal margin of 8S. Inner ridges of 8S of moderate length, pale overall (Fig. 58). Hypogynial valves with straight dorsal margin, not sinuous, and uniformly colored, apices varying from broadly rounded to nearly subacute (Figs. 55, 58). Vaginal apodeme (Fig. 57).

Specimens examined.—Type material: *Tipula incisa* Doane. Lectotype ♂ (WSU): The original description of *incisa* listed four males and one female from Wawawai and two females from Pullman (all Whitman Co., Washington) in the type series. Although the word "Type" appeared following mention of the specimens from Wawawai, no one specimen was so specified. Following the reasoning set forth for designating a lectotype for *impudica*, I hereby designate as lectotype a specimen that Doane labeled uniquely, as follows: "Wawawai 5–7 Wash", "Collector/R.W. Doane", "Type/184" (handwritten in red ink), a red square of paper. My lectotype label is attached. The lectotype lacks the left antenna after flagellomere V and the right antenna after flagellomere III, the right pro- and mesothoracic legs beyond the trochanters and the tarsus of the left prothoracic leg. This lectotype is designated to help stabilize the nomenclature in this group of species. The following specimens are paralectotypes: 1 ♂ and 1 ♀,

topotypic, labeled 5–7–98 (WSU); 2 ♂, topotypic, (CAS, USNM); 1 ♀, Pullman, Washington (WSU). One female from Pullman was not located.

Tipula flavicoma Doane. Holotype ♂ (CAS): Label data, condition and illustrations of some aspects of the genitalia can be found in Byers (1976).

Tipula kansensis Alexander. Holotype ♂ (USNM): KANSAS: Douglas Co., Lawrence, VI-4–1918, CPA. The holotype lacks the right wing and three legs.

Tipula eriensis Alexander. Holotype ♂ (USNM): OHIO: Erie Co., Sandusky, 17-VI-1926, D. LaCroix. A wing, antenna and the hypopygium have been slide mounted.

Tipula incisa queres Alexander. Holotype ♂ (USNM): NEW MEXICO: Sandoval Co., Frijoles Canyon, Bandolier National Monument, 19-VI-1942, J. & G. Sperry. A wing, antenna, leg and hypopygium have been slide mounted.

Tipula incisa picturata Alexander. Holotype ♂ (USNM): ARIZONA: Yavapai Co., Peeple's Valley, V-11–1945, G. Knowlton. A wing, antenna and hypopygium have been slide mounted.

Other specimens: CANADA: BRITISH COLUMBIA: Kamloops, 16-VI-1934, G. J. Spencer, 1 ♂ (UBC); same as preceding but 11-VI-1944, 1f (UBC); Kere-meos, 8-V-1923, P. Vroom, 1 ♂ (USNM); Oliver, 5–28-V [no year], C. Garrett, 14 ♂, 5 ♀ (ANSP, UMAA); same as preceding except 5–27-V-1923, 5 ♂, 3 ♀ (USNM). ONTARIO: Point Pelee, 14–17-VI-1920, JN Bigelow, 4 ♂ (UMAA). USA: ARIZONA: Apache Co., Navajo, Hwy. I-40, 19-VI-1987, Baumann et al., 1 ♀ (BYU); Yavapai Co., Yarnell, Weaver Mtns., 24-V-1937, L. Gloyd, 2 ♂ (USNM), same as preceding but 27-V-7-VI-1939, 4 ♂ (UMAA). IDAHO: Nez Pierce Co., 1 mi W Myrtle, 14-V-1959, Foote, 1 ♂ (USNM). KANSAS: Douglas Co., Lakeview area, about 5 mi NW Lawrence, (250 m), larvae and pupae coll. 6-V-1958, adults emerged 10–14-V-1958, GWB#110, 2 ♂ (UK); Lawrence, 14-V-1960, F. Rohlf #123.6, 1 ♂ (UK); Ellsworth Co., Kanopolis Reservoir, east side, oak woods, 8–9-VI-1983, JKG #267, 3 ♂ (JKG, UK); Kingman Co., 14.5 km W Kingman, 10-V-1984, C. Michener, D. Wahl, J. Wenzel, R. Brooks, 1 ♂ (UK); Pratt Co., 11.3 km S Cairo, 10-V-1984, Michener et al., 4 ♂ (JKG, UK); Rush Co., Timken, 22–30-V-1977, E. May, 5 ♂, 8 ♀ (UK). MICHIGAN: Berrien Co., Stevensville, 29-V-1938, collector unknown, 2 ♂ (UMAA); Van Buren Co., South Haven, 23-VI-1938, C. Sabrosky, 1 ♂, 1 ♀ (UMAA). NEW MEXICO: Catron Co., Datil Well Campground,

1.6 km NW Datil, 7420 ft (2260 m), 14-VI-1979, at light, JKG #3, 1♂ (UK); Grant Co., 15 mi S Silver City, 9-VI-1977, G. Knowlton, W. Hanson, 1♂ (USU); Santa Fe Co., Santa Fe, 2100 m, 25-V-1991, C. Nelson, 1♂ (ANSP). OKLAHOMA: Alfalfa Co., Cherokee, 4-VI-1937, J. Standish, 8♂ (UMAA); without further locality data, 4-V-1948, S. Coppock, 2♂, 1♀ (AMNH); Caddo Co., Hinton, 4-V-1939, 1♂ (UMAA); Cleveland Co., Norman, 357 m, 25-IV-1932, I. Strand, 1♂ (AMNH); same but 7-V-1932, B. McCurdy, 1♀ (AMNH); Comanche Co., Wichita National Forest, 7-11-VI-1926, T. Hubbell, 1♂, 2♀ (UMAA); Harper Co., 4.8 km S Buffalo, 12-V-1984, from *Astragalus lotiflorus*, Michener et al., 1♂ (UK); Logan Co., Crescent, 4-V-1939, J. Standish, 1♂, 1♀ (UMAA); Woods Co., Waynoka, 1-2-V-1936, W. Blair, 1♂, 2♀ (UMAA); 4.8 km N Waynoka, 11-V-1984, Michener et al., 1♂, 2♀ (UK); 1 mi N junction of highways 34 and 64, 5-V-1984, R. L. Huber, 1♂ (UK); Woodward Co., Woodward, (578 m), 11-V-1984, Michener et al., 4♂, 2♀ (JKG, UK); 8 km NE Woodward, 12-V-1984, Michener et al., 15♂, 7♀ (CMNH, JKG, UK). OREGON: Baker Co., no specific locality, 20-VII-1922, L. R. Dice #10, 1♂ (UMAA); Grant Co., John Day Picture Gorge, NW of Dayville, 26-V-1950, K. Fender, 1♂ (USNM). UTAH: Carbon Co., Minnie Maude Creek, near junction Nine Mile Creek, 22-VI-1978, Baumann and Winget, 1♂ (BYU); Garfield Co., Sevier River, near Hatch, 7000 ft (2133 m), 23-VI-1942, CPA, 1♀ (USNM); Summit Co., Kamas, 11-VI-1956, G. Knowlton, 2♂ (UK); Utah Co., Orem, 8-x-1971, S. Clark, 2♂ (BYU); Vineyard, 15-VI-1912, T. Spalding, 1♂ (ANSP). WASHINGTON: Asotin Co., Clarkston, 251 m, 15-V-1912, collector unknown, 1♂ (USNM); Snake River, opposite Clarkston, 3-V-1925, A. Melander, 3♂ (USNM); Benton Co., Kennewick, 108 m, 7-VI-1916, 20-V-1921, 1♂, 1♀ (USNM); Whitman Co., Almota, 22-IV-1977, M. Yamane, 1♂ (WSU); as preceding but 11-V, Doane?, 3♂, 4♀ (USNM); as preceding but without date or collector, 1♂ (UMAA); Yakima Co., Mabton, 3-V-1911, 1♂ (USNM). WYOMING: Lusk, 16-VI-1947, at light, D. Denning, 1♀ (UWL).

Discussion.—Alexander (1946a) considered *incisa* to have four subspecies (*incisa picturata* was later added in 1961) and stated that all these “have the structure of the male hypopygium generally the same but differ in the coloration of the body and wings.” I have examined all of Alexander’s types and those of *incisa* and *flavicomma*, as well as

specimens from nearly throughout this species’ range. I find very little variation in the male hypopygium, as noted by Alexander, and the variation in the body and wing coloration is probably continuous, and not valid for supporting subspecific status. Specimens from western and northern North America tend to be darker brown or gray overall, as noted in the description. Specimens from central United States are more often yellowish brown in body coloration and the wings lack the contrasting pale areas. Some specimens from Kansas and Oklahoma, along with the holotype of *flavicomma* (from “Montana”), have the pale area along the cord obsolete and only a small dark spot at the origin of Rs. The dorsal lobes of the ninth tergum also show variation (Figs. 49–53), with the lobes of specimens from western North America usually strongly produced laterally, those of eastern specimens usually less so.

Given my limited study and the descriptions and illustrations given by Alexander, I conclude that none of his taxa merit even subspecific status. The more darkly colored and patterned forms are represented by the types of *incisa incisa*, *i. queres* and *i. picturata* (all western North America) and *kansensis* and *eriensis* (both from the eastern part of the range). The more yellowish, unpatterned form is represented by the type of *flavicomma* (Montana).

Relationships.—Although hitherto placed in the subgenus *Lunatipula* (Alexander, 1965b), *Tipula incisa* is considered here in the subgenus *Eremotipula*; it is the sister taxon to all the other species of *Eremotipula* combined, sharing several important synapomorphies of the male ninth tergum and adminiculum, and the distinctive sclerotized pattern of the female 8S. The plesiomorphic status of *Tipula incisa* within *Eremotipula* is shown in the male by the sclerotized, not membranous, ventral lobe of A9S, presence of a narrow OD without an anterior extension, and other features, and, in the female, by the straight dorsal margin of the hypogynial valve, and short apodeme of the 10T. The similarity between the male eighth sternum of *incisa* and *melauderiana* is striking but consists of plesiomorphic features such as thickened lateral setae, paired patches of setae and the lack of a membranous lobe.

Geographic distribution.—British Columbia southward to Arizona, eastward to Oklahoma, Kansas and Ontario (Fig. 59).

Seasonal distribution.—Late April to late July; a single record from October. Nearly all adults oc-

cur in May and June in most parts of the range. The earliest known emergence was in southeastern Washington; the October record from Utah is of interest as it is nearly three months later than any other records.

Habitat.—The habitat of *incisa* is different from that known for any other species of *Eremotipula*. George Byers collected larvae and pupae of *incisa* from sandy soil under 2.5–5.0 cm of leaf litter of cottonwood (*Populus deltoides*) in a riparian woodland near an oxbow lake in Douglas Co., Kansas. In Ellsworth Co., Kansas, I collected adult *incisa* in oak woodland with little undergrowth, and sandy soil with a thin layer of detritus. In Rush Co., Kansas, E. May collected teneral individuals in open grassland bordering a riparian woodland. In Garfield Co., Utah, Alexander (1948) reported collecting crane flies (including a female of *incisa*) from the “humid strip close to the water,” mostly grasses, *Equisetum* and low willows, with vast sagebrush areas occurring away from the river. Alexander (1961) reported the types of *incisa picturata* were found “among blue grass and squirreltail grass, in the shade” of several trees. Although there are no records of this species being collected in arid shrubland habitat as is common with the other species of *Eremotipula*, it is certainly found in some of the most xeric woodland habitats frequented by terrestrial *Tipula*.

Little information is available on elevations at which *incisa* occurs, but most specimens are from elevations below 1000 m, even in mountainous parts of western North America. The highest elevation recorded is from Datil Well, New Mexico, at 2260 m.

Tipula (Eremotipula) melanderiana Alexander

Tipula (Eremotipula) melanderiana Alexander 1965a: 360–361; Alexander 1967: 26, figs. 88–89 (9T, vent.; ID, OD, 8S), key; Theischinger & Theowald 1981: 29, cat.

Diagnosis.—Thorax and hypopygium dark reddish brown, with thoracic stripes dark brown and distinct, wing with dark spot at origin of Rs and junction of Sc and R₁. *Male*: 9T dorsal lobes small and triangular, STP short (Fig. 60); 9S with membranous protuberance below base of adminiculum, lobe with conspicuously long microtrichia (Fig. 68); outer basal lobe of ID deeply concave laterally, apex broad, slightly rounded to

subtruncate, with short spur at ventral edge (Fig. 64); 8S with paired patches of dense, short setae (Fig. 67), several lateral setae elongate, thickened and curved toward midline. *Female*: Inner ridges of 8S broad and dark (Figs. 71, 72).

Description.—*Length*: Male 14–17 mm, female 19–25 mm. *Head*: Vertex and postgena dark reddish brown, with dense gray pruinosity; bright orangish areas sublaterally on occiput. Antennal length: male 4–6 mm, female 2–4 mm. *Thorax*: Overall dark reddish brown with dense gray pruinosity, darkest in females. Presutural scutum with two pairs of distinct brown to dark brown stripes, with additional narrow stripe between inner pair, inner pair evenly narrows posteriorly. Postsutural scutum with distinct, reddish brown spots in some males. *Legs*: Yellowish brown (males) to dark yellowish brown (females), tibia brightest. Femoral rings dark brown. Apices of tibiae darkened. *Wing*: Male 16–17 mm long, 4 mm wide, female 14–19 mm long, 3–4 mm wide. Overall light grayish-brown (slightly browner in some individuals—one female with each wing a different shade); stigma dark brown. Small dark brown spots at junction of Sc and R₁ and at origin of Rs. Pale area nearly surrounding stigma, extending as pale band along cord to discal cell, and additional pale streak along M. *Abdomen*: In males, terga overall yellowish brown; sterna and hypopygium dark reddish brown and slightly pruinose, terga 2–6 each with sublateral and dorsal dark brown spots, sometimes lateral spots nearly contiguous longitudinally along abdomen. In females, dorsally dark yellowish brown, with median dorsal patches sometimes confluent as longitudinal line, lateral dark brown patches on terga 1–8 confluent, bordered laterally by gray, sterna mostly dark reddish brown, with distinct dark medial line. Posterior membranous areas on 9T and 9S white and contrasting in males. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.6. Dorsal lobes widely separated, divergent, each lobe small, triangular, width at base about twice length, apex subacute to rounded (Fig. 60). Subtergal process short, ratio of length STP/9T = 0.3, uniformly sclerotized, with smooth dorsal margin, dorsal ridge from near wide, flat base to narrower, rounded apex. Cuticle at base of STP strongly reticulate, reticulate to striate at apex; microtrichia dorsally on basal half. Ventral plate shelf narrow, surface strongly reticulate, with ventral margin plicate. Ventral lobes only partially

concealed beneath dorsal lobes; each lobe narrow and flat (Figs. 61,62). *Ninth sternum* (+ *basistyle*): Basistylar suture complete. Dorsomedial margin with small acute projection near attachment of sp1. Dorsolateral margin of basistyle narrowly rounded projection opposite posterior condyle of inner dististyle. Ventral lobes of A9S with setae uniformly short, not noticeably thickened, and directed laterally (Fig. 62). A nearly quadrate, median membranous protuberance below A9S with conspicuously long microtrichia (Fig. 68). *Outer dististyle*: Posterodorsal margin shallowly concave, anterior extension of moderate length and directed slightly dorsad, posterior corner strongly produced (Fig. 63). *Inner dististyle*: Overall darkly sclerotized. Ventral surface of upper beak with strong ridges, lower beak with fine ridges. Crest large, size equal to body of upper and lower beak (Fig. 64), rounded and overlapping OBL, extended anteriorly along lateral surface of upper beak with groove between crest and upper beak equal to width of lower beak; dorsal margin convex, conspicuously serrulate with surface of crest tuberculate. OBL short, L/W = 1.6–1.9, directed nearly posteriorly, lateral surface deeply concave, mesal surface with well-developed ridge, ventral edge continuing anteriorly as distinct ridge; apical margin slightly rounded to subtruncate but lower edge produced into a short spur, posterior margin of ID produced below OBL. *Adminiculum*: Each lateral plate greatly expanded, perpendicular to median lobe (Fig. 65), with large lobe on either side of dorsal spine along lateral margin (Fig. 66), apex of each lobe rounded, with semicircular striae. Dorsal lobes above and separated from median lobe, each flat, broad, with irregular apical margin. Median lobe narrow, about one-fourth total height of adminiculum, compressed, with large beak. *Eighth sternum*: Posterior (sclerotized) margin with deep, V-shaped, emargination. Membranous apical region with two, low broad protuberances covered with dense, medium length setae (Fig. 67); a sclerite at each side, extending medially, with 2–4 thickened, smooth, elongate setae, curved toward midline and about twice length of other setae on sclerite, remaining setae on sclerite numerous, some smooth. All other setae conspicuously carinate. Medial membranous region without lobe, but sometimes a raised, flat area between lateral sclerites, with short to long, singly-spaced microtrichia, some on tubercles. *Ovipositor*: Eighth tergum brown along basal two

thirds length, yellowish brown apically, with abundant setae. Ninth tergum dark reddish brown and pruinose. Tenth tergum dark reddish brown (evenly colored) and shiny, without pruinosity, only slightly swollen apically. Cerci reddish brown, shiny, apical half gently curved dorsad, with apices extremely narrow. Basal half of eighth sternum dark reddish brown, with grayish pruinosity only basally, anterior half yellowish brown with abrupt boundary at midlength, hypogynial valve blades reddish brown, paler at midlength. Inner ridges of BS well developed, evenly dark brown on lateral surface and in median depressions, median pigmentation not strongly granular nor reaching posterior edge of ridge. Base of fused valvulae (9S) broadened laterally, with several dark setae.

Specimens examined.—*Type material*: Holotype ♂ (USNM): CALIFORNIA: San Bernardino Co., Sheep Creek Canyon, near Phelan, 24-V-1945, A. L. Melander, holotype #11640. The pinned holotype lacks all legs; the right wing, left antenna and hypopygium are mounted on a similarly labeled microscope slide. The ninth tergum and eighth sternum are fragmented and the inner dististyles are compressed. Paratype ♂: CALIFORNIA: San Diego Co., Borrego, 23-IV-1955, R. O. Schuster (pinned specimen is at UCB, and a slide with the left wing and one set of dististyles is in the Alexander Collection at the USNM. The remainder of the hypopygium is missing).

Other specimens: USA: CALIFORNIA: Riverside Co., P. L. Boyd Deep Canyon Desert Research Center, 8.4 km S of Palm Desert, 290 m, 19-IV-1986, at light, JKG #342, 1♂ (UK); same but Marker +21, 5–10-V-1975, T. Egan, S. Swanson, 2♂, 1♀ (UCR); same but 4-V-1974, S. vanVorhis, 2♂ (UCR); same but 1400 ft (427 m), 19-V-1973, M. Quillman, 1♀ (UCR); same but Coyote Creek, 17-V-1975, 1♂ (UCR); same but 0.8 mi N of junction of Deep and Horsethief Creeks, 2960 ft (902 m), 11-V-1974, 16-V-1975, S. vanVorhis, S. Swanson, 2♂, 1♀ (UCR); Idyllwild, San Jacinto Mountains, 15-VI-1940, C. D. Michener, 1♀ (USNM); Millard Canyon (San Bernardino Mtns.), 2500–3000 ft (762–914 m), 26-IV-1969, at light, B. Hunt, C. Howell, 1♂, 2♀ (UCR); vic. Mountain Center, 12-V-1974, S. Frommer, 1♂, 1♀ (UCR); Papett(?) Flat, 12-V-1976, JN Reimer, 1♂ (UCR); Pinyon Flats Campground, 25.7 km SW of Palm Desert, 1221 m, 20-IV-1986, JKG #346, 1♀ (JKG); Santa Rosa Mountain, 31.4 km SW of Palm Desert, 1494 m, 21-

IV-1986, JKG #346, 7♂ (JKG, UK); 27.5 km SW of Palm Desert on CA. Highway #74, 1250 m, 21-IV-1986, most taken at light, JKG #344, 19♂, 9♀ (AMNH, CMNH, JKG, UK); San Bernardino Co., Desert Springs (now Pinon Hills), (1213 m), 19-V-1954, at light, P. H. Timberlake, 1♂ (UCR); Mormon Rocks, 6.4 km N of Lytle Creek, 1067 m, 19-IV-1986, JKG #341, 10♂, 2♀ (CAS, JKG, UK); San Diego Co., Borrego Valley, (235 m), 24-III-1967, R. O. Schuster, 1♂ (UCD); 11.3 km E Julian on Hwy. #78, Banner Queen Ranch, 2800 ft (853 m), no date, C. W. Kirkwood, 2♀ (USNM); Kitchen Creek (S of Mount Laguna), 15-IV-1966, D. G. Denning, 5♂, 1♀ (USNM).

Discussion.—Several discrepancies can be found when comparing the description and illustrations of the male genitalia by Alexander (1965: 360) and those presented here. Alexander states that the dorsal lobes of the ninth tergum are “obtusate, longer than subtergal process, on face of each with more or less sclerotized blade . . .” The ninth tergum on the type slide is fragmented and flattened, and what Alexander describes as the dorsal lobes are, in fact, the projection of the lateral edge of the tergum, with the “sclerotized blade” being the underlying (not directly attached) ventral lobe. The dorsal lobes in this species are shorter than the subtergal process (Fig. 60). The outer basal lobe of the inner dististyle is “semitubular” as stated by Alexander, but his illustration shows a compressed lobe with both lateral and mesal aspects represented. I have not seen any specimens of *melanderiana* with the outer dististyle shaped as in his figure (Alexander 1967: fig. 89).

Although Alexander (1965a) compared *melanderiana* to *utahicola*, the most similar species to *melanderiana* in the structure of the male genitalia is *larreae*. The combination of dark reddish brown body coloration and the dark patterning of the wings is distinctive for *melanderiana* and separates it from *larreae*, as well as all other species of *Eremotipula*. Further distinguishing features are discussed under *larreae*.

Geographic distribution.—Southern California (Fig. 73).

Seasonal distribution.—March 24 to June 15. At Deep Canyon Research Station, Riverside Co., this species has been found over a month-long period, from April 19 to May 19. Adults of *Tipula melanderiana* emerge earlier in the spring than those of most other species in the subgenus.

Habitat.—*Tipula melanderiana* occurs in a variety of habitats in and bordering the Mojave and Sonoran Deserts in California. Specimens have been collected often in the low-elevation *Larrea-Franseria* desert at Deep Canyon, Riverside Co., as well in similar desert vegetation in the Borrego Valley, San Diego Co. I have found *melanderiana* most abundant in chaparral vegetation in mountains bordering these deserts; this includes red shank chaparral (*Adenostoma sparsifolium*) in the Santa Rosa Mountains, and chamise chaparral (*A. fasciculatum*) at Mormon Rocks in the San Bernardino Mountains. In addition, I found *melanderiana* in a pinyon pine-juniper community at Pinyon Flats, Riverside Co. Specimens from near Julian were collected in “high desert” among “live oak, manzanita and yucca” (label data).

This species has been found at elevations from 235 m to nearly 1500 m.

Tipula (Eremotipula) larreae, new species

Diagnosis.—*Male*: Hypopygium similar to that of *melanderiana*; 9T with short dorsal lobes and subtergal process (Fig. 74), ventral lobes narrow and elongate (Fig. 75). Outer basal lobe of ID deeply concave laterally, apex broad, with short spur at dorsal edge (Fig. 76). Adminiculum with dorsal lobes strongly divergent (Fig. 79). 8S with broad band of setae, several lateral setae noticeably thickened and bent mesad; membranous lobe pyramidal, broad and short (Fig. 81). *Female*: faintly streaked wings, usually a brown spot at junction of veins Sc and R₁, inner ridge of 8S scarcely broadened beyond hypogynial valve, dark anteriorly, pale posteriorly.

Description.—*Length*: Male 13–18 mm, female 20–26 mm. *Head*: Vertex and postgena dark brownish gray, sometimes with brighter, orangish sublateral areas on occiput. Antennal length: male 3–5 mm, female 3 mm. *Thorax*: Overall brownish gray; postpronotum sometimes pale and contrasting. Presutural scutum with two pairs of brown to dark brown, longitudinal stripes (no median stripe between inner pair), remainder of scutum densely pruinose. *Legs*: Femoral rings brown to dark brown. Tibial apices slightly darkened. *Wing*: Male 14–16 mm long, 3–4 mm wide, female 15–19 mm long, 4–5 mm wide. Overall light brown; stigma brown and brown spot at junction of Sc and R₁, slightly darker along vein Cu. Clear area surrounding stigma, extending as pale band

along cord into cell m_3 ; indistinct, pale band along A_1 and pale streak in cell a_1 . *Abdomen*: Male bright yellowish brown, shiny; female slightly darker. Terga 2–6 with sublateral and dorsal dark brown patches or lines, forming nearly continuous lateral lines along abdomen in females and some males; area between patches and lateral margin of tergum pale and contrasting, with corresponding dark line along lateral edge of sterna in females. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.6. Dorsal lobes scarcely evident, broadly rounded, 2–3 times as wide as long, margin slightly irregular (Fig. 74). Subtergal process short, ratio of length STP/9T = 0.2–0.3, not compressed, evenly sclerotized, with smooth dorsal margin, rounded apex. Cuticle of STP not reticulate; dorsal microtrichia, extending to apex (visible only at high magnifications). Ventral lobes scarcely concealed beneath dorsal lobes, each flat, narrow, usually curved dorsad (Fig. 75), extending from flat ventral plate, apex subtruncate to falcate. *Ninth sternum* (+ *basistyle*): Dorsomedial margin with short ventral extension opposite attachment of sp1. Dorsolateral margin of basistyle nearly straight opposite posterior condyle of ID. Each ventral lobe of A9S with several short and thickened setae, directed laterally (Fig. 77). *Outer dististyle*: Dorsal margin straight to slightly concave, anterior extension of moderate length and directed dorsad. *Inner dististyle*: Ventral surface of upper beak with strong ridges, lower beak acute to truncate. Crest large, posteriorly overlapping outer basal lobe (Fig. 76), extended anteriorly along lateral surface of upper beak, with groove between crest and upper beak equal to width of lower beak; dorsal margin of crest concave posteriorly and conspicuously serrulate, surface tuberculate. OBL short, L/W = 1.7–1.9, directed posterodorsally, lateral surface deeply concave, mesal surface with well-developed ridge, ventral edge continuing anteriorly as pale ridge, width of lobe increasing to apex, apical margin slightly rounded to subtruncate but upper edge produced into a short spur. *Adminiculum*: Lateral plates expanded basally, gradually narrowing to divergent, narrow, wrinkled dorsal lobes (Fig. 79). Median lobe large (about one-third height of total adminiculum), extended posteriorly (Figs. 78, 80) and expanded laterally, margin rounded, without beak; a pair of ridges flanking ventral margin of lobe. *Eighth sternum*: Yellow bands present, sometimes indistinct. Posterior

(sclerotized) margin deeply concave. Membranous apical region with broad band of long setae narrowly divided at midlength; a thin sclerite at either end of band, with 1–2 thickened, convergent setae, light sclerotization extending medially to surround membranous lobe (Fig. 81). Non-thickened setae carinate. Membranous lobe immediately posterior to setal band nearly pyramidal, about as long as wide, with short microtrichia on tubercles (Fig. 82). *Ovipositor*: 8T brown, pruinose, posterior margin straight. 9T brown and pruinose basally, reddish brown and polished apically. 10T reddish brown and polished, dark along posterior border but not noticeably swollen, length 1.5x width at base. Cerci elongate and slender, L/W = 4.4–6.0, only slightly upturned in apical half, yellowish brown and shiny. 8S brown and pruinose basally and along lateral edges, a reddish brown streak medially and reaching midlength, apical remainder pale but without abrupt boundary between dark and light coloration. Each inner ridge of 8S slightly elevated, lateral surface and cavity brown (Fig. 70), (pale anteriorly at ridge in two specimens; Fig. 69), median cavities brown, reaching only half length of ridge. Hypogynial valve blades typical, light reddish brown, apices a blunt point.

Specimens examined.—*Type material*: Holotype ♂ (UK): CALIFORNIA: Riverside Co., Pinyon Flats Cmpgd, 25.7 km SW Palm Desert, T7S,R5E,sec.10, elev. 1221m, April 20, 1986, J. K. Gelhaus #343. Paratypes: 31♂, 7♀. USA: CALIFORNIA: Los Angeles Co., Littlerock Reservoir, 8.8 km S of Pearland, 1006 m, 18-IV-1986, at light, JKG #340, 2♂ (JKG, UK); Riverside Co., about 0.8 mi N of junction of Deep and Horsethief Creeks, 2960 ft (902 m), 19-IV-1975, R. B. Smith, 1♂ (UCR); topotypic, 20–21-IV-1986, 10♂, 3♀ (JKG, UK, USNM); 27.5 km SW Palm Desert on CA. Hwy. #74, 1250 m, 20–21-IV-1986, several at light, JKG #344, 3♂ (UK); same as preceding but 23km SW, 1150m, 2♀ (ANSP); Joshua Tree National Monument, Ryan Campground, 24.1 km SE Joshua Tree, 1311 m, 24-IV-1986, several at light, JKG #353, 10♂ 1♀ (AMNH, CMNH, JKG, UK); as preceding but White Tank Campground, 17.7 km S of Twenty Nine Palms, 1145 m, 24-IV-1986, JKG #350, 1♂ (UK); Santa Ana Mountains, Cleveland National Forest, 804 m, 27-V-1979, at light, JKG #3, 1♀ (UK); San Bernardino Co., Granite Mountains, "Bunny Club", 25.4 km S of Kelso, 1265 m, 26-IV-1986, at light, JKG #357, 2♂, 1♀ (JKG); as preceding but

Granite Cove, 25.7 km S of Kelso, 1311 m, 25-IV-1986, at light, JKG #355, 3 ♀ (CAS, UK); as preceding but Snake Spring, 23.0 km S of Kelso, 1219 m, 25-IV-1986, dead on surface of pool, JKG #354, 1 ♂ (UK); New York Mountains, 40.2 km NW of Goffs, 1414m, 27-IV-1986, JKG #359, 1 ♂ (UK); San Diego Co., Anzo-Borrego State Park, Culp Valley Campground, 6.5 km W Ranchita, 1036m, 22-IV-1986, at light, JKG #347, 1 ♀ (ANSP).

Etymology.—*Tipula larreae* is named for its association with creosote bush, *Larrea divaricata*, a dominant shrub in the low-elevation deserts that this species of *Eremotipula* inhabits.

Discussion.—The median lobe of the adminiculum in *larreae* has a doubly-pouched appearance in dorsal aspect, which is unique within *Eremotipula* (Fig. 79). The apparent dorsal lobes are wrinkled (Fig. 80), and may in fact be homologues of the striate or wrinkled "lateral lobes" of *melanderiana* (Fig. 66). If this interpretation is correct, the actual dorsal lobes may have become appressed to the median lobe, each lobe forming a lateral pouch, with the lateral lobes then moving into a dorsal position.

Males of *larreae* can be confused with those of *melanderiana* as both share an overall similar morphology of the hypopygium. There are many minor differences between the species, however, and most of these are visible in dried specimens. In addition to those features used in the keys, the male outer basal lobe of the inner dististyle in both species is similarly shaped, but in *larreae*, it is shorter and broader, with a spur on the dorsal, not ventral, edge (Fig. 76). Also, the thickened setae of the male eighth sternum are only slightly longer than the unmodified setae (and sometimes hard to discern in dried specimens), not greatly elongate and conspicuous as in *melanderiana*.

Relationships.—Although *larreae* and *melanderiana* are quite similar in features of the inner dististyle, ninth tergum and eighth sternum, there are no synapomorphies to support a sister-species relationship, and *larreae* is best regarded as being slightly more derived than *melanderiana*, as determined by the phylogenetic analyses.

Geographic distribution.—Southern California (Fig. 83).

Seasonal distribution.—Mid-April to late May.

Habitat.—Although only one specimen of *larreae* was found in museum collections during the initial stages of this study, I discovered this species at many localities in southern California

during fieldwork in 1986. *Tipula larreae* is now known from diverse habitats within and surrounding the Mojave Desert and the western edge of the Sonoran Desert. At the southern edge of its range, at Deep Canyon (Sonoran Desert), it was found in low-elevation desert dominated by creosote bush (*Larrea divaricata*) and burro bush (*Franseria dumosa*). At higher elevations, in the bordering Santa Rosa Mountains, *larreae* occurred among pinyon pine, juniper, and live oak (*Quercus turbinella*). It was also in red shank chaparral (*Adenostoma sparsifolium*) at another site nearby. In the Mojave Desert, I found *larreae* most abundant in a habitat of *Juniperus californica*, blackbrush (*Coleogyne ramosissima*) and Joshua tree (*Yucca brevifolia*), in the Joshua Tree National Monument, but I also found the species widespread in the Granite Mountains in creosote bush desert scrub, and in the New York Mountains among *Juniperus*, *Ephedra*, *Haplopappus* and *Prunus fasciculatum*.

Tipula larreae occurs at a narrow range of elevations, from 900 to 1400 m.

The *eurystyla* Species Group

This species group includes *baumanni*, *eurystyla*, *elverae*, *helferi*, *kirkwoodi*, *maderensis*, *rogersi*, *spinirecta* and *utahicola*. Synapomorphies of this group are given in Fig. 33, with the species showing striking modifications of the male and female genitalia. In particular, the lateral expansion of the cerci, and reduction and subsequent modification of the hypogynial valves, are convergent with that found in female *Tipula* (*Vestiplex*), a quite unrelated subgenus. Perhaps the structures relate to deep oviposition as has been shown to occur in *Vestiplex* (Hemmingsen 1956).

Tipula (*Eremotipula*) *eurystyla* Alexander

Tipula (*Eremotipula*) *eurystyla* Alexander 1969: 8–9; Theowald & Theischinger 1981: 18, cat.

Diagnosis.—**Male:** 9T with STP elongate, strongly upturned, with pale apex (Figs. 86, 88); ID small (Fig. 90), upper beak extremely depressed, crest absent, OBL small and rounded; OD large, club-shaped (Fig. 91); 9S with membranous protuberances near adminicular base (Figs. 92, 93). **Female:** 9T laterally with well-developed tubercle (Fig. 99). Cerci broadly expanded, excavated dorsally, with strong ventral ridge (Figs. 99,

100). Hypogynial valves short, unequally bifid at apex (Fig. 102).

Description.—*Length*: Male 13–15 mm (16–17 mm in alcohol), female 18–22 mm (21–26 mm in alcohol). *Head*: Vertex and postgena grayish yellow. Antennal length: male 4–5 mm. *Thorax*: Overall yellowish gray, pruinose. Presutural scutum with two pairs of light brown, narrow stripes. Pleura bright gray. *Legs*: Femoral rings absent. *Wing*: Male 12–15 mm long, 3 mm wide, female 13–18 mm long, 3–4 mm wide. Overall tinged with light brown; stigma slightly darker. Cells *c* and *sc* faintly yellowed. Pale band along cord indistinct, extending to discal cell. *Abdomen*: Yellowish to yellowish gray. No dark dorsal or lateral markings. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.6. Each dorsal lobe short, broad (Fig. 86), width 6x length, apex truncate to slightly concave, margin slightly crenulate. STP elongate, ratio of length STP/9T = 0.6–0.7, wide and dorsoventrally flattened at base, broadly attached to ventral plates, strongly upturned beyond base (Fig. 88), becoming compressed and pale apically; irregular dorsal margin, venter with slight basal swelling. Cuticle of STP and cavity strongly reticulate (Fig. 89). Ventral plate shelf narrow, broadly fused to STP, smooth (Fig. 87). Ventral lobes concealed beneath dorsal lobes, slightly convergent, each lobe wide at base with rounded sides, narrowing (usually abruptly) at midlength to short rod with truncate apex. *Ninth sternum* (+ *basistyle*): Basistylar suture complete. Dorsolateral margin of BS with small spine opposite posterior condyle of ID, spine smallest in Washington Co., Utah specimens (including holotype), spine bent inward in dried specimens (Fig. 94). Each ventral lobe of A9S rounded, with dense, thickened, short setae directed laterad. Membranous area below A9S with several sets of low protuberances (Figs. 92, 93), largest quadrate and closest to A9S, microtrichia long and conspicuous. *Outer dististyle*: Large, apex club-like, without anterior extension (Fig. 91). *Inner dististyle*: Upper beak extremely depressed, ventral surface with two slight ridges, lower beak broad and twisted laterally. Crest absent, beak and OBL broadly attached (Fig. 90). Basiconic pegs grouped but few in number (about 6). OBL small and rounded, L/W = 1.2, nearly flat, upper edge strongly rotated laterally (90°) with respect to base, without a ridge on lateral surface, apex broad, rounded. Mesal face of basal half of OBL

with patch of fine hairs small. *Adminiculum*: Dorsal lobes small and indistinct, converging above median lobe (Figs. 95, 96). Median lobe small, about one-seventh total height of adminiculum, compressed, with recurved beak; margin below beak deeply concave, a pair of indistinct ridges below median lobe. *Eighth sternum*: Posterior (sclerotized) border deeply emarginate medially. Membranous apical margin with a low and broad, rounded lobe at midlength, smallest in Washington Co., Utah specimens; setal band nearly continuous (microscopically interrupted at midlength), including around median lobe, band only 2–3 setae thick; a sclerite at either end, with one thickened seta, only slightly longer than other, numerous setae. Most setae with carinae (except some lateral setae) (Fig. 98). A minute membranous lobe posterior to setal row, with long, dense microtrichia (Fig. 97). *Ovipositor*: Posterior margin of eighth tergum nearly straight. Lateral area of ninth tergum with well developed tubercle (Fig. 99); sclerite mostly dark brown (as in 10T) sclerotized, not pruinose. 10T relatively short, slightly swollen posteriorly, with distinct setal sockets with short pale setae (Fig. 99). Longitudinal apodeme complete. Cerci broadly expanded laterally, excavated medially, with outer edge upturned, smooth to irregular in outline (Figs. 99, 100). Ventral ridge of cerci strongly developed. Hypogynial valves short, bifid (Fig. 102); inner ridges of 8S low and pale (Fig. 101). Vaginal apodeme as in Fig. 101.

Specimens examined.—*Type material*: Holotype ♂ (USNM): UTAH: Washington Co., Dixie State Park, IV-24-1968, G. F. Knowlton & D. W. Davis, holotype #12410. Right antenna, right wing, one leg and hypopygium are mounted on a microscope slide; all other legs missing except the right prothoracic and part of the right metathoracic leg. Microscope slide similarly labeled as pinned specimen.

The type locality, "Dixie State Park", is shown as "undeveloped" on a 1963 Utah highway map, as "Dixie-Snow Canyon State Park" on a similar 1965 map, and as "Snow Canyon State Park" on current maps. It is approximately 1036 m in elevation.

Other specimens: 11♂, 17♀. USA: ARIZONA: prob. Navaho Co., Shanto Canon (Shonto?), 6500 ft (1981 m), 16-VI-1949, JN Cricknar, 1♂, 9♀ (ANSP, USNM). UTAH: Kane Co., Coral Pink Sand Dunes State Park, (56 km NW Kanab, 1829 m) 4-

VI-1981, R. W. Baumann, 5♂, 6♀ (ANSP, BYU, USNM); same as preceding but: 1828 m, no date, C. van Nidek, 2♀ (Amsterdam); Utah Co., Utah Lake (about 1400 m), east side, 19-V-1963, D. E. Elwell, 1♂ (BYU); Washington Co., Leeds Canyon, 27-29-IV-1985, N. N. Youssef, 1♂ (USU); same as preceding but 26-V-1974, W. Hanson, G. Knowlton, 1♂ (USU) (probably), Zion National Park, 20-V-1946, collector unknown, 2♂ (BYU).

Discussion.—I found minor differences among the specimens as noted above. The Washington Co., Utah male specimens have very small, bent basistylar spines, smaller and not so circular outer basal lobes, and the membranous protuberances on the ninth sternum and along the posterior border of eighth sternum are not so produced.

Relationships.—*Tipula eurystyla* stands isolated within the *eurystyla* group, but the similarity of the adminiculum, and the medium expansion of the male 8S border in *eurystyla*, *utahicola* and *baumanni* may indicate a close relationship. The bifid apices of the female hypogynial valves are unique in the subgenus.

Geographic distribution.—Central Utah to northern Arizona (Fig. 103).

Seasonal distribution.—April 24 to June 16.

Habitat.—*Tipula eurystyla* has rarely been collected and little is known regarding its habitat; elevation range is 1400–1981m. The vegetation of Coral Pink Sand Dunes State Park, Kane Co., Utah, includes juniper, pinyon pine, deciduous oak, *Artemisia tridentata* and *Chrysothamnus* sp. I found no evidence of this species when I collected in the park in early May 1986.

Tipula (Eremotipula) utahicola Alexander

Tipula (Lunatipula) utahicola Alexander 1948: 32–34, fig. 11 (wing; hypo., lat; 9T; ID; OD; 8S; A9S); Alexander 1965b: 39, cat.; Theischinger & Theowald 1981: 47, cat.

Diagnosis.—*Male*: 9T with dorsal lobes scarcely evident and broad (Fig. 105), ventral lobes elongate and narrow (Fig. 106); STP short, smooth, uniformly sclerotized, and upturned beyond base; OD extremely small, scarcely reaching lower beak of ID; ID lacking membranous crest (Fig. 109); midventral area of 9S with small membranous protuberance covered with conspicuously long microtrichia (Fig. 111); 8S with straight, membranous, apical margin, setal band with a

thick, elongate, mesally curved, twisted seta on either end (Fig. 113). *Female*: unknown.

Description.—Based on 2 males and description by Alexander (1948). *Length*: Male 12–14 mm. *Head*: Vertex and postgena brownish gray, with a pair of sublateral yellowish patches on occiput. Antennal length: male 4–5 mm (described by Alexander, 1948, as 1.2 mm). *Thorax*: Overall brownish gray, pruinose. Presutural scutum with two pairs of brown stripes, area between inner pair of stripes bluish gray. *Legs*: Femoral rings indistinct. Apices of tibiae narrowly darkened. *Wing*: Male 13 mm long, 3 mm wide. Light brown clouds in distal sections of cells r_{1+2} , r_3 , m_1 – m_3 , and most of anal cells; stigma brown. Most of cells r_5 , m_4 and r pale, with pale band along cord from stigma to discal cell. *Abdomen*: Indistinct dark sublateral lines on terga 2–5. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.6. Dorsal lobes scarcely evident, slightly produced medially, margins smooth (Fig. 105). STP uniformly sclerotized, short, ratio of length STP/9T about 0.2, upturned slightly, wide and dorsoventrally flattened, slightly narrowing to rounded, smooth apex. Cuticle of STP and cavity strongly reticulate. Posterolateral margin of tergum (at sides of dorsal lobes) scarcely emarginate. Ventral surface of shelf smooth, margin rugose, ventral lobes only slightly concealed beneath dorsal lobes (Figs. 105, 106), slightly convergent, each lobe elongate, narrow and flat, with nearly truncate apex. *Ninth sternum* (+ *basistyle*): Dorsolateral margin of BS produced into large, thick, subacute spine opposite posterior condyle of ID. Ventral lobes of A9S membranous, with dense, thickened, short laterally-directed setae (Fig. 107). Paired membranous protuberance midventrally below A9S (Fig. 111), with conspicuously elongate microtrichia. *Outer dististyle*: Small, posterodorsal margin straight, with short anterior extension. *Inner dististyle*: Dorsum of upper beak broad, ventral surface of upper beak without ridges. Lower beak large, with rounded apex. Crest absent posteriorly (Fig. 110), but a sclerotized lamella along lateral surface of upper beak (Fig. 109), anterior half of ID and OBL divided by a depressed pale shelf. Outer basal lobe of medium length, L/W about 2.0, slightly concave laterally and strongly bent laterad, apical margin broad, slightly concave, with lower edge produced. *Adminiculum*: Similar to that of *eurystyla* in most details. Lateral plates and dorsal lobes completely fused, meeting above median

lobe. Median lobe small, about one-seventh to one-eighth total height of adminiculum, flat, with recurved beak. *Eighth sternum*: Posterior (sclerotized) border deeply emarginate. Apical (membranous) border straight, with broad band of setae, narrowly interrupted medially (Fig. 113), setae slightly increasing in length laterally; a sclerite at either end of band with a single broad, flat seta and other thinner setae; each broad seta strongly bent and curved mesad, much longer than other numerous setae on sclerite, twisted several times along its length in holotype. Most setae in band carinate. Membranous lobe small and broad, slightly sclerotized overall, with many short microtrichia.

Specimens examined.—*Type material*: Holotype ♂ (USNM): UTAH: Millard Co., White Valley, 1-V-1940, Station 1, in tent, Jane C. Dirks no. 53, holotype #7699. The left antenna, both wings, one leg and hypopygium are mounted on a similarly labeled microscope slide. The left mesothoracic leg is still attached to the body, the remaining four are absent. The type locality, White Valley, is located near the Millard/Juab Co. boundary, between the Confusion and House Ranges, about 104 km west of Delta, Utah.

Other specimens: USA: UTAH: Tooele Co., Johnson's Pass, 21-V-1954, H. E. Cott, 1♂ (UMAA).

Discussion.—Some inconsistencies appear when comparing the description and illustrations of Alexander (1948) and those presented here; these are due in part to the distorted slide mount of the male hypopygium used by Alexander. The pair of thickened lateral setae of the eighth sternum are not exactly as shown by Alexander (1948: fig. 11); although bent as depicted, each seta (in the holotype) is also twisted five complete revolutions along its length (Fig. 113). Also, the shape of the outer basal lobe is not as drawn by Alexander (1948). The species (and the closely related *baumanni*), has a unique lamella along the lateral surface of the beaks of the inner dististyle, possibly homologous to the crest. The "crest" referred to by Alexander (1948) may be the produced edge of the dorsum of the upper beak.

Relationships.—*Tipula utahicola* is clearly a member of the *eurystyla* species group, evidenced by the morphology of the adminiculum. It appears to be the sister species of *baumanni*, based on a close similarity in the male genitalia, particularly the sclerotized lamella on the inner dististyle, a feature found only in these two species.

Geographic distribution.—West central Utah (Fig. 103).

Seasonal distribution.—May.

Habitat.—No information on the habitat is associated with the type specimen, but Fautin (1946) considered the shadscale (*Atriplex confertifolia*) community to predominate in the White Valley, with subdominant shrubs of winterfat (*Ceratoides lanata*) and bud sage (*Artemisia spinescens*).

Tipula (Eremotipula) baumannii, new species

Diagnosis.—Species extremely similar to *utahicola* but differing in the following characteristics: Wings strongly marked with brown coloration. *Male*: 9T with ventral lobes elongate and narrow (Fig. 115), exceeding STP in length, and apex subacute; apical membranous margin of 8S medially convex (Fig. 116). *Female*: unknown.

Description.—Based on 3 males (all in fluid). *Length*: Male 16.0 mm, 22.0 mm. As in *utahicola* except: *Head*: Vertex and postgena yellowish brown. Antennal length: male 4 mm. *Thorax*: Overall yellowish brown, pruinosity not observable. Presutural scutum with two pairs of brown stripes. *Legs*: Femoral rings indistinct. Apices of tibiae narrowly darkened. *Wing*: Male 13–14 mm long, 4 mm wide. Distinct brown clouds in distal sections of cells r_{1+2} and r_3 , a broad brown band from cells m_1 to cu , a broad brown triangle in cell a_1 and most of cells r , m and a_2 brown; stigma brown. Most of cells r_5 and cu pale, with pale band along cord from stigma to discal cell. *Abdomen*: Dark sublateral and dorsal lines on terga 2–5 present or absent; a ventral line present in one male. *Hypopygium*: *Ninth tergum* (Fig. 115). Ratio of length 9T/BS = 0.5. Posterior margin of tergum at sides of dorsal lobes slightly emarginate. Ventral lobes (Figs. 114, 115) elongate (extending past STP), narrow, flat, and tuned slightly dorsad, lobes narrowing gradually to subacute apices. *Inner dististyle*: Ventral surface of upper beak with two ridges. Lower beak large, with truncate apex. Outer basal lobe of medium length, L/W about 2.3, lateral surface reduced, with mesal setae actually extending dorsally, upper edge produced (Fig. 114). *Eighth sternum*: Membranous apical border convex medially, forming a broad lobe, with broad band of setae, 2 elongate, broad bend setae on each side (Fig. 116), Membranous lobe not slightly sclerotized overall, with many short microtrichia.

Specimens examined.—*Type material*: Holotype ♂ (BYU): CALIFORNIA: Inyo Co., Big Pine Creek, 7-VI-1986, at light, R. Baumann and D. Giuliani. Paratypes: Topotypic, 2♂ (ANSP, BYU).

Relationships.—*Tipula baumannii* is closely related to *T. utahicola* and *eurystyla*, as evidenced by a similar distinctive morphology of the adminiculum, and appears to be the sister species of *utahicola* (see relationship section for that species).

Geographic distribution.—East central California (Fig. 83).

Seasonal distribution.—Early May.

Habitat.—No information on the habitat is associated with the type specimens.

Tipula (Eremotipula) elverae, new species

Diagnosis.—Known from female only. Extremely large species (up to 30 mm long). Terga 2–8 with broad, nearly triangular lateral patches, these nearly confluent with median lines posteriorly on terga (Fig. 117). Cerci broadly expanded, excavated dorsally, with strong ventral ridge (Fig. 118). Hypogynial valves minute, each apex single, and rounded (Fig. 119). Lateral border of 8S gently rounded, without well-developed, outwardly-projecting lateral flange (Fig. 119).

Description.—*Length*: Female 28–30 mm. *Head*: Vertex and postgena dark brownish gray; a pair of reddish or orangish, circular sublateral spots on occiput. Antennal length: female 4 mm. *Thorax*: Overall dark brownish gray and pruinose, with membranous areas contrasting and pale. Presutural scutum with two pairs of contrasting, dark brown stripes, median pair abruptly narrowing posteriorly; area between median stripes chestnut brown. *Legs*: Dark yellowish brown, with distinct brown femoral rings and faint terminal tibial rings. Tibial spur formula 1:2:2. *Wing*: Female 19–21 mm long, 5 mm wide. Wings faintly variegated with light brown, stigma brown. Cells *c* and *sc* pale and yellowish. Outer ends of cells r_{1+2} , r_3 and discal cell, and most of cells m_1 – m_3 and a_2 , and junction of veins Cu and crossvein m-cu light brown, with triangular light brown patches in cells *m* and a_1 . Remainder of wing pale, nearly clear. *Abdomen*: Extensively variegated with yellowish brown and brown. Tergum 1 entirely brown, remainder of terga 2–8 with brown dorsal median line and broad, nearly triangular lateral patches, these nearly confluent with median lines posteriorly on terga (Fig. 117).

Ovipositor: Posterior margin of eighth tergum slightly concave. Lateral area of ninth tergum with only low swelling (a small tubercle found on one side of one individual only); sclerite mostly dark brown (as in 10T), sclerotized, not pruinose. 10T moderately long, length about 1.5x posterior width, slightly swollen and paler posteriorly, with distinct setal sockets with erect pale setae (Fig. 117). Longitudinal apodeme complete. Cerci robust, broadly expanded laterally, excavated medially, with outer edge smooth in outline (Figs. 117, 118); entire length gently curved upwards and narrowing evenly to acute apices. Ventral ridge of cerci strongly developed (Fig. 118). Eighth sternum flattened, with gently rounded lateral border, without a distinct medial flange (Fig. 118); inner ridges of 8S low, short, entire area pale, without pigmentation, and no distinct setae (Fig. 119). Each hypogynial valve a short lobe with narrowly rounded apex (Fig. 119).

Specimens examined.—*Type material*: Holotype ♀ (ANSP): UTAH: Piute Co., Tushar Mountains, City Creek Campground, 10.2 km NW Junction, 2320 m, 30-VI-1991, J. Gelhaus #528. Paratype: 1♀, Tooele Co., Little Valley Cr., Little Valley Campground, Sheeprock Mountains, 2134 m, 19-VI-1980, R.W. & S.W. Baumann and S. Vernon, in fluid (BYU).

Etymology.—This species is named for my grandmother, Elvera Steinmeyer Gelhaus, who encouraged my interest in insects from an early age.

Discussion.—The male of this species is unknown, and most likely remains uncollected, as the female does not appear to belong to any of the known species of the *eurystyla* group, due to strong differences in body and wing patterning and coloration, or geographic distribution. *Tipula utahicola* is the only Utah species of the *eurystyla* group for which the female stage remains to be associated. The male of *utahicola* is much smaller than would be expected due to normal differences between sexes (12–14 mm vs. 28–30 mm long), and lacks the contrasting coloration of the thorax and abdomen of the females described above.

Relationships.—The laterally expanded cerci and minute blades of the hypogynial valves are both female characters shared by other members of the *eurystyla* group (where known). The simple hypogynial valve blade, and strongly contrasting coloration of the body are similar to that found in

helferi, although neither feature is interpreted here as a synapomorphy.

Geographic distribution.—Western Utah.

Seasonal distribution.—June 19–30.

Habitat.—The habitat of the Piute County site is dominated by ponderosa pine, pinyon pine, juniper, scrub oak, curl-leaf mountain mahogany with understory shrubs of Great Basin sagebrush, rabbitbrush (2 spp.) and *Opuntia* sp.

Tipula (*Eremotipula*) *helferi* Alexander

Tipula (*Eremotipula*) *helferi* Alexander 1965a: 358–360; Alexander 1967: 26, fig. 84 (9T, ID, OD, Adm.), key; Theischinger & Theowald 1981: 21, cat.

Diagnosis.—Wings patterned with light brown and pale streaks (Fig. 444). *Male*: 9T (Figs. 120, 121) lacking dorsal and ventral lobes and with minute STP (difficult to see in dried, unmacerated specimens); median furrow reduced; dorsolateral margin of BS with large spine; ID with anterior half of body and OBL broadly fused (Fig. 122), and without crest, OBL with crenulate, dorsal margin and of unusual shape. *Female*: 9T laterally with well-developed tubercle (Fig. 128). Cerci broadly expanded, excavated dorsally, with strong ventral ridge (Figs. 127, 128). Hypogynial valves minute, each apex single, and rounded (Fig. 130). Lateral border of 8S with well-developed, outwardly projecting, lateral flange (Figs. 129, 130).

Description.—*Length*: Male 14–18 mm (holotype “about 12 mm”), female 24–26 mm. *Head*: Vertex and postgena dark brownish gray; a pair of reddish or orangish, circular sublateral spots on occiput. Antennal length: male 4–5 mm, female 3 mm. *Thorax*: Overall dark brownish gray and pruinose, with membranous areas contrasting and pale, orangish areas on pronotum and meron. Presutural scutum with two pairs of contrasting, chestnut brown to dark brown stripes, median pair abruptly narrowing at midlength. Area between median stripes often lighter grayish-brown. *Legs*: Usually dark yellowish brown, sometimes brown. Femoral rings dark brown, sometimes strongly contrasting. Legs of female noticeably stouter than male. *Wing*: Male 12–16 mm long (holotype wing “11.5 mm” long), 3–4 mm wide, female 16–18 mm long, 3–4 mm wide. Wings extensively variegated with light brown and white, stigma brown (Fig. 444). Cells *c* and *sc*

faintly yellowed. Outer end of cells r_{1+2} , r_3 , discal cell, cells m_1 – m_3 and a_2 , and end of vein Cu light brown, with triangular light brown patches in cells *m* and a_1 . Remainder of wing pale. *Abdomen*: Overall mottled yellowish brown and shiny; tergum 1 and lateral and posterior margins of all other terga pale and contrasting. Terga 1–8 with dark brown dorsal and sublateral patches, forming nearly complete lines along abdomen. Male ninth tergum and eighth sternum dark brown, female ninth and tenth tergum, and cerci dark brown and polished, female ninth sternum pale. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.6. Dorsal lobes absent (Fig. 120), posterior margin divided into truncate halves by shallow median furrow, posterolateral margin produced slightly into smooth narrow plate (probably remnant of ventral plate shelf), cuticle yellow around bases of some short, pale setae. STP a minute point, ratio of length STP/9T about 0.05; cuticle sclerotized without reticulations but with dorsal microtrichia. Posterolateral margin of tergum without emargination. Ventral plate without cavity, ventral lobes or developed shelf (Fig. 121); marginal band short and medial (and attached to sp_2), lateral margin of ventral plate plicate. *Ninth sternum* (+ *basistyle*): Sp_2 with anterior half strongly bent medially (Fig. 123). Dorsolateral margin of BS produced into large, broad and thickened spine opposite posterior condyle of ID, apex narrowly rounded. Ventral lobes of A9S with dense, erect, slightly thickened pale setae, slightly longer than dorsal lobe setae. *Outer dististyle*: Posterodorsal margin straight, anterior extension short. *Inner dististyle*: Upper beak flattened with striations only vaguely present dorsally, weak ridges ventrally. Lower beak with smooth, rounded apex, slightly curved laterally. Crest absent, beak and outer basal lobe broadly attached and not divided by a depressed pale shelf (Fig. 122). OBL broad and flattened, L/W = 1.3, upper edge bent strongly laterad with respect to base of ID; dorsal margin crenulate, no ridge on lateral surface, apical region narrowed. Mesal surface of OBL with abundant long setae, patch of short fine hairs absent. *Adminiculum*: Lateral plates narrowly expanded throughout, fused with rounded, separated dorsal lobes, flanking median lobe (Fig. 124), with a small flap or ridge at base (Fig. 125). Median lobe small, about one-seventh total height of adminiculum, with short beak. Posterior margin of adminiculum immediately below median

lobe concave; a pair of dorsoventral ridges flanking margin near base. *Eighth sternum*: Yellow longitudinal bands present, usually strongly contrasting. Posterior (sclerotized) margin shallowly concave. Membranous apical region with band of sparse, long setae, interrupted at midlength; a narrow sclerite with several setae at either end of band, none noticeably thickened. A few setae in band with indistinct carinae. A minute membranous lobe immediately posterior to setal row, with microtrichia (Fig. 126). *Ovipositor*: Posterior margin of eighth tergum slightly concave. Lateral area of ninth tergum with well developed tubercle (may be difficult to see in dried specimens); sclerite mostly dark brown (as in 10T), sclerotized, not pruinose. 10T relatively short, only slightly longer than wide, slightly swollen and paler posteriorly, with distinct setal sockets with short pale setae (Figs. 127, 128) Longitudinal apodeme complete. Cerci robust, broadly expanded laterally, excavated medially, with outer edge smooth to irregular in outline (Fig. 128); entire length gently curved upwards (Fig. 127). Ventral ridge of cerci strongly developed. Eighth sternum flattened, laterally produced at midlength into distinct outer flange (Figs. 127, 130); each inner ridge of 8S low but elongate, overall brown except pale median area (Fig. 129). Hypogynial valves minute, each apex simple and rounded (Figs. 129, 130).

Specimens examined.—*Type material*: Holotype ♂ (CAS): CALIFORNIA: Kern Co., Short Canyon, 6 mi W of Inyokern, 1036 m, 11-IV-1954, J. W. MacSwain. The type is on permanent loan to the California Academy of Sciences from the University of California at Berkeley (California Insect Survey). The hypopygium is mounted on two slides, one with the left inner and outer dististyles, the other with the remainder of the structures. Most of the hypopygium is in good condition, but the adminiculum is mounted with the dorsal side facing up (as illustrated in Alexander 1967: fig. 84), and the eighth sternum is torn.

Other specimens: 54♂, 3♀. USA: CALIFORNIA: Inyo Co., Goodale Creek, (45 km NW of Lone Pine), 3-IV-1953, H. B. Leech, from *Salix exigua* flowers, 1♂ (CAS); Kern Co., Freeman Canyon, 14.5 km W of Inyokern, 1372 m, 14-15-IV-1986, many taken at light, 53♂, 3♀, JKG #339 (ANSP, AMNH, CAS, CMNH, UK, USNM, UMAA).

Relationships.—Alexander (1965a) allied *Tipula helferi* to *Tipula (Lunatipula) degeneri* and suggested that *degeneri* may belong in *Eremotipula* as

well. Although there is a superficial resemblance between the two species in terms of the ninth tergum, basistylar lobe and inner dististyle, *degeneri* lacks all the synapomorphies of *Eremotipula* and appears to be a much more basally derived species (along with the closely related *mercedensis*) and not a close relative of *helferi*.

Tipula helferi, along with *spinerecta*, have reduced or lost many features of the 9T normally associated with species of *Eremotipula*. However, this species also possesses a number of unique synapomorphies of *Eremotipula* not likely to have evolved convergently, and *helferi* seems clearly to be a member of *Eremotipula*, albeit a rather apomorphic species of an early lineage.

The highly apomorphic nature of male *helferi* makes it difficult to place even as a species of *Eremotipula*, unless the hypopygium is examined in detail. The ventral lobe of the appendage of the ninth sternum, the adminiculum (if visible) and the posteriorly directed outer basal lobe of the inner dististyle help in routine determinations to subgenus, and the structure of the ninth tergum and inner dististyle allows easy specific determination. The minute subtergal process is rarely visible in a dried, unmacerated specimen.

Geographic distribution.—East central California (east side of Sierra Nevada; Fig. 83).

Seasonal distribution.—April 3–15.

Habitat.—The vegetation at the type locality, Short Canyon, consists mostly of blackbrush (*Coleogyne ramosissima*) and other shrubs, scattered Joshua trees (*Yucca brevifolia*) and *Opuntia* sp. I was unable to find any *helferi* when I visited the canyon in 1986. In Freeman Canyon, only a few kilometers south but much larger and longer than Short Canyon, I found *helferi* in abundance, among *Artemisia tridentata*, *Ephedra* sp., *Haplopappus linearis*, *Chrysothamnus* sp. and *Yucca brevifolia* (Joshua Tree Woodland, Vasek & Barbour 1977).

Tipula (Eremotipula) spinerecta Alexander

Tipula (Lunatipula) spinerecta Alexander 1947: 70–71; Alexander 1965b: 39, cat., Alexander 1967: 46, fig. 120 (9T, ID, OD, apex of basistyle, 8S), key; Theischinger & Theowald 1981: 41, cat.

Diagnosis.—Wings patterned with light brown and pale streaks (Fig. 445). *Male*: 9T (Fig. 132) with short, dorsal lobes, and lacking a well developed ventral plate and lobes. (Fig. 131); STP

short and mostly membranous, with rounded apex (difficult to see in dried, unmacerated specimens); dorsolateral margin of basistyle with polished, black erect spine (Fig. 136); ID (Fig. 135) without typical crest but with pale spine near juncture of beak and OBL; OBL with broad, rounded apex. *Female*: unknown.

Description.—Based on 6♂. *Length*: 15–17 mm. *Head*: Vertex and postgena dark brownish gray; a pair of reddish or orangish sublateral spots on occiput. Antennal length 3.5–4.0 mm (“4.5 mm”, Alexander 1947). *Thorax*: Overall gray, with membranous areas yellowish. Presutural scutum with two pairs of contrasting chestnut brown stripes, area between median pair of stripes gray, rarely dark gray or with median thin line (holotype). *Legs*: Dark yellowish brown with dark brown femoral rings. *Wing*: 14–16 mm long (“16–17 mm” Alexander, 1947), 3–4 mm wide. Wing indistinctly variegated with light brown and white; stigma light brown (Fig. 445). Cells *c* and *sc* clear. Outer end of cells *r*, *r*₁₊₂, *r*₃, *m*, *m*₂, *m*₄, *cu* and anal cells light brown, remainder pale. *Abdomen*: Terga 1–8 with dark brown dorsal and sublateral patches, dorsal patches forming nearly continuous line along abdomen; remainder of abdomen yellowish. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5. Dorsal lobes short, broad, L/W = 0.4, with apices subacute to acute, margin smooth (Fig. 132). STP short, about equal to length of DL, sclerotized dorsally at base, remainder membranous with rounded apex (Figs. 132, 133); membrane with short microtrichia. Cuticle of area near plate finely reticulate. Posterior margin of tergum at sides of dorsal lobes broadly emarginate. Ventral plate shelf extremely narrow (scarcely evident), without a distinct ventral lobe (Fig. 131). *Ninth sternum*: Basistylar suture complete. Dorsolateral margin of BS with large, broad erect spine opposite posterior condyle of ID (Fig. 136), margin of spine blackened and smooth. Each ventral lobe of A9S somewhat extended, with many erect yellowish setae, a few dorsal setae appearing coarser than remainder and directed slightly laterad (Fig. 137). Membranous midventral region distinctly swollen from near A9S to acrosternite (Fig. 137), area with short microtrichia. *Outer dististyle*: Posterodorsal margin straight, anterior extension short, posterior corner slightly produced (Fig. 136). *Inner dististyle*: Upper beak slightly depressed, ventral surface with ridges, lower beak digitiform, separated from upper beak (Fig. 135).

Typical crest mostly absent, but triangular, mostly membranous lobe arises perpendicular to beak, near juncture of beak and OBL. Outer basal lobe of moderate size, L/W = 1.6, mostly flat, directed dorsoposteriorly; lobe increasing in width slightly to midlength, apex broad and rounded (cf. *incisa*). A small shelf protrudes on lateral surface near midlength. *Adminiculum*: Each dorsal lobe pale, small, apex subtruncate (Fig. 134). Median lobe small, with distinct short beak; dorsally with a short spine. *Eighth sternum*: Posterior (sclerotized) border nearly straight. Membranous apical margin with band of long subequal setae, none noticeably thickened (Fig. 136); band narrowly interrupted medially; a thin sclerite at either end of band. Setae in band with only weakly developed carinae. “Membranous lobe” small, about 2x as wide as high, conical and mostly darkened, with abundant microtrichia, some shortened. Surrounding membrane slightly tuberculate, with scattered microtrichia.

Specimens examined.—*Type material*: Holotype ♂ (CAS), CALIFORNIA: Kern Co., Cuyama Valley, 10-IV-1932, E. P. Van Duzee. The holotype lacks the left antenna and both hind legs. Paratypes: 3♂, topotypic (USNM).

Other specimens: **USA: CALIFORNIA**: Same locality and date as type, 1♂ (CAS); Kern Co., 19 mi E Bakersfield, 24–26-III-1947, P. H. Arnaud, Jr., 1♂ (USNM).

Relationships.—Alexander (1947) noted the similarity of *spinerecta* to some species in the *impudica* group, but maintained the species in the subgenus *Lunatipula* even after the description of the subgenus *Eremotipula* (Alexander 1965 a,b). *Tipula spinerecta* clearly belongs within *Eremotipula* even though the species lacks the synapomorphy of a ventral plate and lobes of the ninth tergum; a similar reduction is found in *helferi*. *Tipula spinerecta* does possess a subtergal process, albeit somewhat modified from that seen in other species, the ventral lobe of the appendage of the ninth sternum is typical for the subgenus, including the presence of some thickened setae, and the adminiculum has dorsal lobes, not curved hooks as in *Lunatipula* s. str. The shape of the outer dististyle and presence of a membranous lobe between the eighth and ninth sterna are also typical features of the subgenus. Several characters place it clearly in the *eurystyla* group, including a reduced crest, erect spine on the basistyle and swollen midventral region of the ninth sternum.

Geographic distribution.—Southern California (southern foothills surrounding the Central Valley; Fig. 83).

Seasonal distribution.—March 24 to April 10.

Habitat.—No information on the habitat of *Tipula spinerecta* is associated with the few known specimens.

Tipula (Eremotipula) kirkwoodi Alexander

Tipula (Lunatipula) kirkwoodi Alexander 1961: 82–84; Theowald & Theischinger 1981: 24, cat.

Diagnosis.—Wing with conspicuous, longitudinal white streaks along cells *m* and *r*₅, and along cell *cu* and anal cells (Fig. 442). *Male*: 9T with dorsal lobes scarcely evident (Fig. 140), ventral lobes elongate, flat with truncate apices (Fig. 142); STP short, smooth, uniformly sclerotized, with bilobed plate at base (Fig. 140); Basistyle with broad, nearly triangular lobe opposite posterior condyle of ID (Fig. 138); ID without membranous crest, outer basal lobe elongate, with posterior edge emarginate subapically (Figs. 143, 144); mid-ventral area of 9S with small membranous protuberance covered with conspicuously long microtrichia. *Female*: unknown.

Description.—Based on two males and description of Alexander (1961). *Length*: "about 20 mm". *Head*: Vertex and postgena grayish brown. Antennal length: male "about 5.5 mm." *Thorax*: Overall grayish brown. Postsutural scutum with two pairs of brown stripes. Pleura light gray. *Legs*: Femoral rings absent. *Wing*: Male 18.5–19.0 mm long, 4.9–5.0 mm wide. Overall strongly contrasting brown and white pattern, stigma not distinct (Fig. 442). Cells *c* and *sc* yellowish brown. White longitudinal stripes from arculus to cell *r*₅ and along proximal portions of cell *a*₂, *a*₁ and *cu*; additional white areas comprising most of cells *m*₃ and *m*₄ (includes all distal medial cells in non-type specimen) and distal portion of *r*₃; remainder of wing brown. *Abdomen*: Dark yellowish brown. No dark dorsal or lateral markings. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS not measurable. Each dorsal lobe short, broad (Fig. 140), width 2.5x length, apex slightly to strongly concave, medial margin slightly crenulate. A pair of small rounded lobes dorsally at base of STP (Fig. 140). STP uniformly sclerotized, short, ratio of length STP/9T = 0.3, wide and dorsoventrally flattened, apical margin rounded and smooth. Cu-

ticle of STP and cavity strongly reticulate. Posterior margin of tergum at sides of dorsal lobes not emarginate. Ventral plate shelf narrow, ventral lobes each large, broad and flat with truncate apex (Fig. 142). *Ninth sternum* (+ *basistyle*): Basistylar suture complete. Dorsolateral margin of BS with large, broad, nearly triangular lobe opposite posterior condyle of ID (Fig. 138). Each ventral lobe of A9S small, with slender, erect and pale setae, slightly longer than dorsal lobe setae. Membranous area below A9S with rounded protuberance and long microtrichia. *Outer dististyle*: Posterodorsal margin straight, anterior extension of moderate length, posterior corner strongly produced. *Inner dististyle*: Upper beak depressed, ventral surface without ridges, lower beak broad. Crest absent. Outer basal lobe elongate (Fig. 143, 144), L/W = 4.0–5.5 (because of slide mount, base difficult to measure), flat overall, lobe directed dorso-posteriorly, narrow at base, increasing in width to midlength, posterior margin strongly emarginate beyond midlength, apex broad and rounded. Mesal face of OBL, particularly along anterior edge, with setae short (about half length of those seen posteriorly) and mixed with the short fine hairs, with those setae extending along apical margin particularly short (Fig. 144). *Adminiculum*: Each dorsal lobe small and indistinct, apex apparently truncate (Fig. 141). Median lobe moderate in size, about one-third total height of adminiculum, appearing expanded dorsally, sclerotized and with surface uniquely tuberculate; beak short. *Eighth sternum*: Posterior (sclerotized) border notched medially. Membranous apical margin with broad band of setae, narrowly interrupted medially; a sclerite at either end of band with three broad, flattened and elongate setae, and other narrower and shorter setae; elongate setae curved mesad. Setae in band carinate. Membranous lobe distinct (Fig. 139), about as long as wide, and lightly sclerotized; microtrichia short, on tubercles. Surrounding membrane at base of lobe tuberculate and bare.

Specimens examined.—*Type material*: Holotype ♂ (UNSM): ARIZONA: Pima Co., Santa Rita Mountains, Madera Canyon, 1463 m (4800 ft), 23-IV-1961, C. W. Kirkwood. The left antenna, right wing and foreleg, and hypopygium are mounted on a microscope slide.

Other specimens: USA: ARIZONA: Same locality as type except 1493 m (4900 ft), 28-IV-1962, 1♂ (USNM).

Relationships.—Although not previously placed in *Eremotipula*, *Tipula kirkwoodi* clearly belongs in the subgenus, possessing the synapomorphies of a ventral plate shelf and lobe, and subtergal process of the ninth tergum, and lateral plates of the adminiculum. The species is closely related to others in the *eurystyla* group, evidenced, for example, by the basistylar lobe shape, lack of a crest on the inner dististyle and a membranous protuberance on the ninth sternum.

Geographic distribution.—Southern Arizona (Fig. 103).

Seasonal distribution.—April 23–28.

Habitat.—No information on the habitat of *Tipula kirkwoodi* is associated with the two specimens, but Madrean evergreen woodland (dominated by *Quercus* spp.) predominates at the elevations given (Brown 1982b).

Tipula (Eremotipula) rogersi, new species

Diagnosis.—Wing with conspicuous, longitudinal streak along cells *m* and *r*₅, and along cell *cu* and anal cells. *Male*: 9T with dorsal lobes small, STP short, and ventral lobes scarcely evident (Figs. 152, 153); basistyle with large, broad spine opposite posterior condyle of ID (Fig. 148); ID without a distinct crest (Fig. 151), outer basal lobe elongate, increasing in width apically, setae absent near apex on mesal surface (Fig. 145); mid-ventral area of 9S with rounded membranous protuberance (Figs. 148, 149); apical margin of 8S with single thickened seta at each end of setal band, length equal to other setae in band (Fig. 149). *Female*: unknown.

Description.—Based on 2 males (via absolute alcohol and xylol). *Length*: 17–18 mm. *Head*: Vertex and postgena grayish brown. Antennal length: male 5 mm. *Thorax*: Overall grayish brown. Post-sutural scutum with single pair of brown stripes or stripes absent. Pleura light gray. *Legs*: Femoral rings indistinct. *Wing*: Male 15 mm long, 4 mm wide. Wing patterning as in *kirkwoodi* except light brown, not brown. *Abdomen*: Yellowish brown. Terga 2–5 with distinct dorsal brown line and lateral brown patches. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.28. Each dorsal lobe small and triangular (Figs. 147, 153), width about 2× length, apex pointed and slightly downturned. STP uniformly sclerotized, short, ratio of length STP/9T = 0.3, equally narrow nearly throughout, apex rounded and curved dorsally. Cuticle of STP

and cavity not reticulate. Posterior margin of tergum at sides of dorsal lobes emarginate. Ventral plate shelf narrow with irregular margin (= ventral lobes), each side with three small dentitions (Fig. 152). *Ninth sternum* (+ basistyle): Basistylar suture complete. Dorsolateral margin of BS greatly expanded posteriorly into huge triangular lobe opposite posterior condyle of ID, apical margin subacute, glabrous and strongly sclerotized; a strong carina extending to apex (Fig. 148). Each ventral lobe of A9S small, with slender, yellowish setae, longest and most erect setae near apex (Fig. 145). Membranous area below A9S swollen overall, with large rounded protuberance anteriorly (near acrosternite), protuberance slightly expanded apically, with short microtrichia (Figs. 148, 149) (cf. *kirkwoodi*). *Outer dististyle*: Posterodorsal margin straight, anterior extension of moderate length, posterior corner strongly produced (Fig. 148). *Inner dististyle*: Upper beak depressed, ventral surface with ridges, lower beak broad with truncate apex (Fig. 151). Crest absent. Outer basal lobe elongate, L/W = 3.0, flat overall, narrowed and directed dorsoposteriorly at base, abruptly increasing in width subapically, apex broad with mesal edge rounded (Figs. 151, 145). Mesal face of OBL with pale setae only, very short setae along dorsal edge; short fine hairs in typical grouping, but with a few hairs scattered apically. *Adminiculum*: Each dorsal lobe small, with apex an acute point (Fig. 146). Additional pair of sharp spines posterior to dorsal spine. Median lobe small, about one-fourth size of total adminiculum, with short beak, a pair of flanges basally. *Eighth sternum*: Posterior (sclerotized) border concave. Membranous apical margin with broad band of setae; a sclerite at either end of band, with a single thick seta (Fig. 149); length of seta equal to those in band. "Membranous" lobe distinct, about as long as wide, and lightly sclerotized throughout (Fig. 149); spinules on low tubercles (Fig. 150). Surrounding membrane at base of lobe tuberculate and bare.

Specimens examined.—Type material: Holotype ♂ (UMAA): ARIZONA: Santa Cruz Co., Coronado National Forest, 16-IV-1950, at light, R. R. Miller et al. The hind legs are no longer attached to specimen; one leg is glued to the specimen point. Paratype: 1 ♂, ARIZONA: Santa Cruz Co., Kane Ranch, 17-IV-1950, R. R. Miller et al. (ANSP).

Relationships.—*Tipula rogersi* is well supported as the sister species of *maderensis* (Fig. 33).

Geographic distribution.—Southern Arizona (Fig. 103).

Seasonal distribution.—April 16–17.

Habitat.—No information on the habitat of *Tipula rogersi* is associated with the two known specimens.

Tipula (Eremotipula) maderensis, new species

Diagnosis.—Wing with conspicuous, longitudinal white streak along cells *m* and *r*₅, and along cell *cu* and anal cells. *Male*: 9T with dorsal lobes scarcely evident and STP short (Fig. 157), ventral lobes elongate, flat with truncate apices (Fig. 158); basistyle with erect, elongate, narrow spine opposite posterior condyle of ID (Fig. 154); ID with small membranous crest, outer basal lobe elongate, with apex broad and slightly rounded, without short setae near apex (Fig. 159); midventral area of 9S with small membranous rounded protuberance. *Female*: unknown.

Description.—Based on one male. *Length*: 20 mm. *Head*: Vertex and postgena grayish brown. Both antennae broken. *Thorax*: Overall grayish brown. Postsutural scutum with stripes absent. Pleura light gray. *Legs*: Femoral rings absent. *Wing*: Male 18 mm long, 4 mm wide. Wing patterning as in *kirkwoodi*. *Abdomen*: Yellowish brown. Terga 2–5 with lateral brown patches. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.41. Each dorsal lobe small (Fig. 157), width about 2x length, apex with small median point. STP uniformly sclerotized, short, ratio of length STP/9T = 0.3, equally narrow nearly throughout, apex narrowly rounded (Figs. 157, 158). Cuticle at base of STP reticulate. Posterior margin of tergum at sides of dorsal lobes emarginate. Ventral plate shelf narrow, lobe of moderate length and equal width throughout, apex truncate (Fig. 158). *Ninth sternum* (+ *basistyle*): Basistylar suture complete. Dorsolateral margin of BS expanded posteriorly into elongate, straight, narrow spine opposite posterior condyle of ID; a darkened excavated area posterior to spine (Fig. 154). Each ventral lobe of A9S small and rounded, with slender, yellowish setae (Fig. 154). Membranous area below A9S swollen overall, with small rounded protuberance anteriorly (near acrosternite), with short microtrichia (cf. *kirkwoodi*). *Outer dististyle*: Posterodorsal margin straight, anterior extension of moderate length, posterior corner strongly produced (Fig. 154). *Inner dististyle*: Upper beak de-

pressed, ventral surface with faint ridges, lower beak with narrowly rounded apex (Fig. 159). Crest small in extent, moderately developed posteriorly. Outer basal lobe elongate, L/W = 3.0, flat overall, lobe directed laterally (Fig. 154), narrowed subapically, apex broad and slightly rounded (Fig. 159). Mesal face of OBL with pale setae and short fine hairs in typical grouping. *Ad-miniculum*: Each dorsal lobe small, with two subequal spines (Figs. 155, 156). *Eighth sternum*: Posterior (sclerotized) border concave. Membranous apical margin with broad band of moderate-length setae; a small sclerite at either end of band, with a single thick seta (Fig. 154); length of thick seta about twice that of those in band. Setae in band with carinae. "Membranous" lobe scarcely developed, with three sides, and lightly sclerotized throughout; spinules on low tubercles. Surrounding membrane at base of lobe tuberculate and bare.

Specimens examined.—*Type material*: Holotype ♂ (USNM): ARIZONA: Pima Co., Santa Rita Mountains, Madera Canyon, 7-VI-1952, collector unknown. Only the right prothoracic leg remains attached; an additional leg is glued to the specimen point. Both antennae are broken.

Relationships.—*Tipula maderensis* is the sister species of *rogersi* (Fig. 33).

Geographic distribution.—Southern Arizona (Fig. 103).

Seasonal distribution.—Early June.

Habitat.—No information on the habitat or elevation of *Tipula maderensis* is associated with the single known specimen.

Tipula (Eremotipula) macracantha Alexander

Tipula (Lunatipula) macracantha Alexander 1946b: 49–51; Alexander 1965b: 37, cat.; Alexander 1967: 26, figs. 86–87 (hypo., lat; 9T, vent.; ID; OD; A9S; 8S, inner), loc.; Theischinger & Theowald 1981: 27, cat.

Diagnosis.—Wings overall light brown, patterned extensively with paler bands along cord, in cell *r*₅, along *A*₁ and in cell *a*₁ (Fig. 455). *Male*: 9T with dorsal lobes attenuate, usually slightly exceeding STP in length, STP nearly completely sclerotized (Fig. 160); ventral lobe of A9S small and slightly curled (Fig. 162); outer basal lobe of ID small, concave laterally, with broad, subtruncate apex (Fig. 163). *Female*: Additional ridge lateral to each inner ridge of 8S, both dark overall, lateral

ridge higher than inner, with anterior end abrupt and truncate (Figs. 168, 169).

Description.—*Length*: Male 12–15 mm (specimen in alcohol 16 mm), female 15–22 mm. *Head*: Vertex and postgena dark brownish gray; bright orangish sublateral patches present on occiput. Antennal length: male 3–5 mm, female 3 mm. *Thorax*: Overall brownish gray, pruinose, membranous areas white and contrasting. Presutural scutum with two pairs of dark brown stripes, median pair narrowing posteriorly, orange area sometimes outlining posterior half of medial pair of stripes. *Legs*: Femoral rings brown, distinct (females examined have brown femora, tibia lighter). *Wing*: Male 11–14 mm long, 3–4 mm wide; female 12–16 mm long, 3–4 mm. Overall light brown; stigma brown. Pale area surrounding stigma, extending as pale band, often broad, along cord into discal, m_3 and m_4 cells, also pale spots in cells r_5 and m_1 , rarely in distal section of r_3 . A large, pale spot along middle portion of A_1 , with narrow streak in cell a_1 (Fig. 455). *Abdomen*: Mottled yellowish and brown, shiny. Terga 2–7 with dorsal and sublateral dark brown spots, spots usually forming nearly continuous lines along abdomen, particularly in females. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5. Dorsal lobes widely separated, slightly divergent, long, attenuate, usually extending slightly past apex of STP (Fig. 160), length 1.3–1.7× width at base, margin nearly smooth, apex acute and usually slightly downturned. STP of medium length, ratio of length STP/9T = 0.4–0.5, process depressed basally, slightly compressed apically, dorsal margin smooth. Cuticle of STP faintly reticulate laterally, basal area areolate to rugose, blade rugose. Ventral surface of shelf areolate or rugose, margin plicate, ventral lobes mostly concealed beneath dorsal lobes (Fig. 161), slightly convergent; each lobe narrow, smooth, with slightly rounded to subacute apex. *Ninth sternum* (+ *basistyle*): Dorsolateral margin of basistyle only slightly produced opposite posterior condyle of inner dististyle. Each ventral lobe of A9S small, rounded, with distal border curved outwardly (Fig. 162), with mostly short, thickened setae proximally. *Outer dististyle*: Dorsal margin straight, anterior extension short. *Inner dististyle*: Ventral surface of upper beak with strong ridges, apex of lower beak truncate. Crest pale, small, rounded posteriorly with scattered spinules, dorsal margin serrulate (Fig. 163). OBL short, L/W = 1.3–1.5, directed posterodorsally with apical edge curled laterally, lat-

eral surface deeply concave, with ventral edge continuing anteriorly as a ridge; apex broad, its margin rounded to subtruncate, slightly rounded. *Adminiculum*: Each lateral plate expanded basally, with small dorsal process near lateral margin on either side of dorsal spine (Fig. 166), lateral plates strongly narrowed apically beyond processes. Dorsal lobes separated, small, pale, along sides of median lobe, with smooth, rounded apices (Fig. 165). Median lobe small, about one-fifth height of total adminiculum, with smooth margin, beak absent, slight dorsoventral ridges on either side of posterior margin below median lobe. *Eighth sternum*: Yellow bands pale, indistinct. Posterior (sclerotized) margin concave. Membranous apical region with a broad band of long setae, band extending narrowly cephalad at midlength; small lateral sclerite with several setae at either end of band. Setae on lateral sclerites straight, without carinae; all other setae with carinae and with apical third of each seta twisted. A minute to small, rounded membranous lobe with spinules (Fig. 167) immediately posterior to long setae. *Ovipositor*: 8T brown; posterior margin scarcely concave. 9T reddish brown, shiny posteriorly. 10T reddish brown, shiny, somewhat darker and slightly swollen along posterior border. Longitudinal apodeme dark, broadest just beyond midlength (as viewed laterally). Cerci elongate, flat and relatively broad dorsally, brown overall; scarcely curved dorsad along apical half. 8S brown anterolaterally, reddish brown anteromedially, posterior half paler, strongly contrasting in one specimen. Hypogynial valve blades light brown, apices narrowly rounded (Fig. 169). Each inner ridge of 8S slightly developed anteriorly, indistinct posteriorly, pigmentation darkest along inner side, but longest on lateral surface; an additional ridge laterally (Fig. 169), height exceeding inner ridge, anterior end abrupt and truncate (when viewed dorsally a slightly rounded “pocket” or cavity formed, Fig. 168). Vaginal apodeme expanded dorsally, nearly diamond shaped. Spermathecae dark.

Specimens examined.—*Type material*: Holotype ♂ (USNM): ARIZONA: Mohave Co., Peach Springs, 1460 m, 8-V-1945, G. Knowlton. The holotype lacks all but two legs, one glued to the thorax and the other removed, along with the left wing, left antenna and hypopygium, to a microscope slide, labeled as pinned specimen. Most genitalic structures are minimally distorted and torn.

Other specimens: **USA: ARIZONA:** Coconino Co., Grand Canyon National Monument, 25-IV-1958, rock holes on water, L. Nielson, 9♂ (ANSP, USNM); Pima Co., Baboquivari Canyon, 9-IV-1963, P. H. Timberlake, 1♂ (UCR); Pinal Co., Florence, 19-IV-1927, J. Maitlin, 1♀ (CAS); Maricopa Co., Canyon Lake, (1660m), 22-III-1935, collector not listed, 1♀ (USNM). **CALIFORNIA:** Inyo Co., Death Valley National Monument, Day Light Pass, 1534m, 28-V-1978, J. & R. Brown, 1♀ (AMNH); San Bernardino Co., Granite Cove, Granite Mountains, 15.8 mi SW of Kelso, (1311 m) 15-IV-1962, C. A. Toschi, 1♂ (hypopygium missing), (UCB); Granite Pass (12.5 mi S of Kelso), 3840-4320 ft (1170-1316 m), 27-IV-1968, some at UV light, E. I. Schlinger and others, 4♂, 2♀ (UCR, UK); New York Mountains, 9 km E, 6.5 km S Cima, 1515m, 27-IV-1986, JKG #358, 1♀ (ANSP); New York Mountains, 1939, M. Van Duzee, 1♀ (CAS); Providence Mountains, 4-5-IV-1934, G. & J. Sperry, 3♂ (AMNH). **NEVADA:** Nye Co., Mercury National Testing Site, 11-18-IV-1961, no collector listed, 1♂, 1♀ (BYU); Co.?, Ash Fork, 15-V-1985, at light, W. Chamberlain, 1♀ (TAMU). **UTAH:** Washington Co., Leeds, 22-IV-1968, G. Knowlton, 1♂ (hypopygium missing), 1♀ (USNM); Pintura, 3500 ft (1067 m), 23-IV-1952, O. Bryant, 1♂ (CAS); Santa Clara, 16-IV-1962, G. Knowlton, 1♀ (USNM); St. George, 14-15-IV-1962, 1♂ (hypo. missing), 4♀ (USNM); St. George, (878 m), 3-VIII-1969, J. L. Petty, 1♂ (BYU); Snow Canyon State Park, 19-IV-1986 & 3-V-1984, R. Baumann, M. Whiting, 2♂ (BYU). Several of the above records were determined as *macracantha* by C. P. Alexander, but the male hypopygia are missing and I cannot verify the identity of these specimens. Fortunately, I have nearby records for this species which could be verified.

Discussion.—Certain aspects of Alexander's original description require clarification. The ventral lobes of the ninth tergum do appear spinous in the slide-mounted holotype, although this was not seen in other specimens. The "spinous point" on the basistyle must refer to the sp2 which appears this way on the type slide.

The membranous lobe between the eighth and ninth sterna shows variation in size and sclerotization, with the lobe minute and unsclerotized in specimens from St. George, Utah, and Pima Co., Arizona, and longer with irregular sclerotization in the holotype specimen from Mohave Co., Arizona.

Adults of *macracantha* can be determined most easily by those characters used in the keys, but also the coloration of body and wings, the small size of this species, and its occurrence in lower elevation desert.

Relationships.—Although the exact relationships varies among the cladograms, *Tipula macracantha* is always placed in an isolated position among the more derived species groups. The presence of similar dorsal processes on the aedeagus in *macracantha*, *artemisiae* and the *kaibabensis* group (e.g., *dimidiata*, *schusteri*), although treated as a parallelism here, may imply a grouping encompassing all these species.

Geographic distribution.—Southwestern Utah to southern Arizona, westward to southeastern California (Fig. 103).

Seasonal distribution.—Early April to late May. The collection date of August 3 for a specimen from St. George, Utah is anomalous, considering that all other specimens were collected in the spring, and the low elevation and hot, dry summers of the region would appear to make larval development during the summer impossible. If the record is accurate, then *macracantha* may produce two generations per year when conditions are suitable.

Habitat.—The few records for *macracantha* suggest it is a species of lower elevation (878–1534 m) desert habitats. The vegetation at Granite Cove, Granite Mountains, California, is Mohave desert scrub (Turner, 1982), with dominant shrubs of creosote bush (*Larrea tridentata*), mormon tea (*Ephedra viridis*), catclaw (*Acacia greggii*) with desert almond (*Prunus fasciculatum*) along the wash. Granite Pass, located nearby, has similar vegetation, with the addition of scattered junipers. All known localities in Utah also fall within the area of Mojave desert scrub. Brown (1982a) considers the type locality, Peach Springs, Arizona, to lie within Great Basin Conifer Woodland (pinyon pine-juniper).

Tipula (Eremotipula) artemisiae, new species

Diagnosis.—Male: 9T dorsal lobes widely separated, divergent, small and triangular (Fig. 170); outer basal lobe of ID deeply concave on outer surface (Fig. 172), with well-developed ridge along lower margin; eighth sternum with sparse setae along apex; membranous lobe minute (Fig. 175). Female: low pale inner ridge of 8S (Fig. 271);

small species (cf. *inaduna*). Distributed in eastern Oregon and northwestern Nevada.

Description.—*Length*: Male 12–15 mm, female 17–18 mm. *Head*: Vertex and postgena brown to dark brown, densely pruinose; a pair of sublateral, yellowish patches on occiput. Antennal length: male 4–5 mm, female 2 mm. *Thorax*: Overall yellowish brown to brown, pruinose. Presutural scutum with two pairs of brown to dark brown stripes, medial area between stripes often concolorous with lateral areas, sometimes pruinose, a thin yellowish line often between medial and lateral pairs of stripes; lateral stripes usually bordered with gray. *Legs*: Femoral rings brown, distinct. Tibial apices slightly darkened. *Wing*: Male 12–15 mm long, 3–4 mm wide. Female 12–14 mm long, 3–4 mm wide. Overall light brown; stigma scarcely darker. Pale area surrounding stigma and extending as band along cord, scarcely contrasting. *Abdomen*: Terga 2–5 with sublateral, brown to dark brown, often contiguous patches. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5. Dorsal lobes widely separated, divergent, small, twice as broad at base as long, apex subacute (Fig. 170); inner margin slightly roughened. STP of moderate length, ratio of length STP/9T = 0.4–0.5, slightly depressed with slight dorsal ridge at base; narrowed and pale subapically, with smooth to slightly serrate dorsal margin. Cuticle of STP not reticulate, process faintly plicate. Ventral lobes not concealed beneath dorsal lobes, subparallel (Figs. 170, 171); each lobe broad, flat, with narrowly rounded to subacute apex. Ventral surface of plate reticulate to rugose, margin plicate. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of BS with small projection opposite attachment of sp1. Dorsolateral margin of BS opposite posterior condyle of ID scarcely produced. Ventral lobes of A9S with numerous, short, thickened, laterally-directed setae. *Outer dististyle*: Posterodorsal margin nearly straight, anterior extension of moderate length. *Inner dististyle*: Ventral surface of upper beak and entire apex of lower beak with well-developed ridges. Crest pale (Fig. 172) with scattered spinules, dorsal margin slightly concave, crest rounded posteriorly; a slight groove between crest and beak. OBL short, L/W = 1.5–1.7, directed posterolaterally, deeply concave on lateral surface; well-developed ridge extending from ventral edge, with few dark setae along ridge and scattered elsewhere; apex rounded to subtruncate.

Adminiculum: Lateral plates expanded basally, gradually narrowing dorsally (Fig. 173), a small dorsal process on either side of dorsal spine (Fig. 174). Dorsal lobes slightly divergent and completely separated, pale, rounded, with lateral ridge. Median lobe large, height one-fourth or more of total adminiculum, without distinct beak; a slight dorsoventral carina on either side near beak area, and also flanking posterior margin below median lobe. *Eighth sternum*: Yellow bands distinct. Posterior (sclerotized) margin shallowly biconcave. Membranous apical region with sparse band of moderately long, pale setae, band weakly complete or interrupted medially, mostly 1–3 setae thick but sometimes extending cephalad at midlength; a minute sclerite with few setae at either end of row. Setae without carinae; setae less than half length of sternum 8. Membranous lobe minute (Fig. 175), sometimes divided; width slightly greater than height, with microtrichia singly or in groups. *Ovipositor*: Each inner ridge of 8S low and poorly developed without lateral pigmentation (Fig. 271). Vaginal apodeme slender and scarcely expanded dorsally.

Specimens examined.—*Type material*: Holotype ♂ (USNM): OREGON: Harney Co., Trout Creek, Trout Creek Mountains, 23 May, 1950, K. M. Fender. The type specimen is in good condition, missing only the left pro- and mesothoracic legs. Paratypes: 9♂, 3♀. NEVADA: Washoe Co., "Pah Rah Mountains" (= Rah-Rahgre Range?), SW edge of Pyramid Lake, 4500 ft (1372 m), 8-IV-1951, I. La Rivers, 1♂ (USNM). OREGON: Deschutes Co., 20 mi E of Brothers, 19-VI-1967, R. M. Brown, 1♂ (CAS); Harney Co., Pueblo Mountains, 22–23-V-1950, K. Fender, 3♂, 1♀ (UK, USNM); Pike Creek, Steens Mountains, 23-V-1950, K. Fender, 1♂, 1♀ (USNM); topotypic, K. Fender & Jewett, 3♂, 1♀ (ANSP, USNM).

Etymology.—The specific epithet is derived from the plant genus *Artemisia*, and reflects the close association of this and other species of *Eremotipula* with semi-arid vegetation dominated by *Artemisia tridentata* (big sagebrush).

Discussion.—As noted in the description, appreciable variation is seen in the development of the membranous lobe and setal band of the eighth sternum. The lobe varies from undivided to divided into two or three protuberances, and the setal band may be weakly complete or interrupted medially. In light of the constancy of other geni-

tal features, this variation appears to be intraspecific only.

The small body size, nearly unicolorous wing, distribution in Oregon and Nevada, and several male genitalic features can be used to separate *Tipula artemisiae* from similar species in the *sinistra* and *kaibabensis* groups as noted in the key. Females of *artemisiae* are not easily distinguishable from some regional species, particularly those in the *madina* species group, and the key should be used with caution. The nearly unicolorous wing, without any streaking, will distinguish this species from *impudica* and *spaldingi*; in addition, the high inner ridge of the 8S found in *spaldingi* is clearly distinct from the low ridge found in *artemisiae*. I can only offer a size difference to distinguish *artemisiae* from *madina*.

Relationships.—*Tipula artemisiae* is not clearly referable to any particular species group based on male characters, although it does appear to belong among the more derived species groups. Possibilities are discussed in the phylogenetic analysis section for *Eremotipula*.

Geographic distribution.—Eastern Oregon to northwestern Nevada (Fig. 331).

Seasonal distribution.—April 8 to June 19.

Habitat.—No habitat data are available with any of the specimens. All localities fall within the Northern Great Basin region as described by McKenzie (1982) who gives information on the vegetational profile of the Steens Mountains, where two specimens of *artemisiae* have been collected (at Pike Creek). Pike Creek is located on the east slope of the Steens Mountains between approximately 1524–2134 m; this elevational range encompasses several vegetational zones, with *Artemisia tridentata* dominant at lower elevations, and *A. arbuscula* and *Juniperus occidentalis* at higher elevations.

Tipula (Eremotipula) schusteri Alexander

Tipula (Eremotipula) schusteri Alexander 1965a: 362–363; Alexander 1967: 26–27, fig. 92 (9T, ID, OD, 9S, Adm, 8S), key, loc.; Theischinger & Theowald 1981: 39, cat.

Diagnosis.—*Male*: elongate dorsal lobes of 9T, slightly curved downward with acute apices (Fig. 176); OBL short, sharply curved outwardly and concave laterally, apex subacute (Fig. 179); ventral lobe of A9S with 8–10 stout setae (Fig. 178); apex

of 8S not straight, but forming rounded medial lobe (Fig. 182). *Female*: unknown.

Description.—*Length*: Male 16–18 mm. *Head*: Vertex and postgena dark brown (light brown in holotype); irregular orangish patches sublaterally on occipital region. Antennal length: male 4–5 mm. *Thorax*: Overall brown, pruinose. Presutural scutum with two pairs of contrasting, dark brown stripes, medial pair narrowing posteriorly; median area between inner stripes brown and pruinose. *Legs*: Femoral rings brown and indistinct. Tibiae with darkened apices. *Wing*: Male 14–16 mm long, 3–4 mm wide. Overall light brown; stigma brown. Pale area surrounding stigma, extending as band along cord to discal cell with pale streaks along vein A_1 and in cell a_1 . *Abdomen*: Mottled yellowish brown and brown, shiny terga 2–6 each with medial and sublateral dark brown patches, nearly contiguous along abdomen; sublateral markings greatly reduced in some individuals. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.6. Anterior border distinct medially. Dorsal lobes divergent, each elongate, length 1.5× width at base, narrowing to strongly acute apex (Fig. 176); medial margin irregular, lateral margin smooth. Apical half of each dorsal lobe curved slightly downward. STP elongate, ratio of length STP/9T = 0.6–0.8, basally depressed, apically compressed. Dorsum of STP pale along apical fourth with margin scarcely serrulate. Cuticle of STP near base reticulate, distally striate, with base of blade areolate. Edge of 9T with upper corner often slightly produced (cf. *anasazi*), remainder of margin straight. Ventral surface of shelf areolate, margin irregular. Ventral lobes concealed beneath dorsal lobes, slightly subparallel (Fig. 177); each lobe short, subacute to nearly truncate at apex, with strong ventral ridge. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of BS pale, except abruptly darkened posteriorly, with slightly produced point at midlength opposite attachment of sp1. Dorsolateral margin of BS greatly produced opposite posterior condyle of ID, with rounded margin. Ventral lobe of A9S with 8–10 stout, reddish brown setae along dorsal edge (Fig. 178), setae slightly curved apically; a few moderately thickened, straight setae on mesal edge of lobe. *Outer dististyle*: Posterodorsal margin nearly straight, short to very short anterior extension. *Inner dististyle*: Ventral surface of upper beak with weak ridges, apex of lower beak with several strong ridges.

Crest (Fig. 179) pale, upper margin slightly concave and serrulate, with narrowly rounded lobe posteriorly. OBL small, L/W = 1.7–1.9, concave on lateral surface, slight ridge ventrally, apical region curved outwardly, apex subacute. *Adminiculum*: Each lateral plate narrow; small dorsal process with striae on either side of dorsal spine. Dorsal lobes of lateral plates fused basally, apically separated and divergent, each lobe rounded, wrinkled. Median lobe small posteriorly (Fig. 180), posterior margin straight, without beak. *Eighth sternum*: Yellow longitudinal bands distinct. Posterior (sclerotized) margin usually shallowly concave. Membranous apex with short rounded lobe medially (Fig. 182), bearing an irregular band of setae, about 7–8 setae thick and slightly wider at both ends and at midlength, each end of band with sclerite. Setae over half sternal length, carinate (Fig. 184). A pale, ligulate, membranous lobe immediately postero-medial to setae and concealed between the eighth and ninth sterna (Fig. 183), lobe not visible externally; lobe about 1.5x as long as wide, with singly placed microtrichia.

Specimens examined.—*Type material*: Holotype ♂ (CAS): CALIFORNIA: San Bernardino Co., Victorville, 1-V-1953, G. A. Marsh, R. O. Schuster. The deposition of the holotype is stated in Alexander (1965) as CIS (= California Insect Survey, UCB), but the type is now on permanent loan to the California Academy of Sciences, San Francisco. The right antenna, one leg and terminal segments of abdomen (minus one dististyle) are mounted on one microscope slide; the right wing and an inner dististyle are mounted on a separate slide. Missing entirely from the specimen are all legs (beyond the trochanters) of the left side and middle leg of right side; remaining wing torn along costa at midlength. Of the slide-mounted parts, the ninth tergum is compressed dorsoventrally, both inner dististyles are compressed with one folded over upon itself and distorted completely, adminiculum with apex bent to one side and lateral plates distorted.

Other specimens: USA: CALIFORNIA: Kern Co., Freeman Canyon, 14.5 km W of Inyokern, 1372 m, 14-IV-1986, at light, JKG #339, 5♂ (CAS, JKG, USNM); same but 15-IV-1986, 1♂ (UK); Riverside Co., Joshua Tree National Monument, Ryan Campground, 24.1 km SE Joshua Tree, 1311 m, 24-IV-1986, at light, 1♂ (UK).

Discussion.—Alexander (1965a) failed to mention the presence of the membranous lobe be-

tween the eighth and ninth sterna, or any particulars regarding the structure of the adminiculum. Both parts are visible on the holotype slide. Discrepancies between the illustrations of Alexander (1967) and those presented here are due in part to distortion of the slide-mounted genitalia of the holotype. Alexander's figure of the ninth tergum shows only the posterior half of this sclerite and combines dorsal and ventral views. The inner dististyle shows a mesal aspect and the drawing of the basistyle illustrates the dorsolateral margin opposite the posterior condyle of the inner dististyle. Most puzzling is the unlabelled structure with an aristate apex; this apparently is a distorted view of the sp2 sclerite.

Males of *schusteri* are relatively easy to recognize using the characters listed in the key and diagnosis, particularly the structure of the inner dististyle. The convex margin of the eighth sternum which forms a slight lobe in *schusteri* is seen elsewhere in *eurystyla* (a long lobe occurs in *pellucida*), but *eurystyla* is quite different in most other features. Other structures of the male which allow recognition of *schusteri* include the elongate dorsal lobes and thickened ventral lobes of the 9T, expansion of the lateral margin of the basistyle and the broad membranous lobe (which is not observable in dried, unmacerated specimens).

Relationships.—The production of the apical margin of the eighth sternum, along with the overall shape and strongly curved orientation of the outer basal lobe of the ID in males of *schusteri* and *pellucida* suggest that these two taxa may be sister species. (A produced margin of the eighth sternum is also found in *eurystyla*, but otherwise this species does not appear closely related to either *schusteri* or *pellucida*). Unfortunately, the autapomorphic nature of most features of the male genitalia in *pellucida* obscures homologies which might further clarify its relationship with *schusteri*.

Geographic distribution.—Southeastern California (Mojave Desert) (Fig. 315).

Seasonal distribution.—April 14 to May 1.

Habitat.—Habitat data are available for two of the three sites where *schusteri* is known to occur. At Freeman Canyon, I found shrubby vegetation of *Artemisia tridentata*, *Ephedra* sp., *Chrysotliamnis* sp. and *Haplopappus linearis* predominating, with scattered Joshua trees (*Yucca brevifolia*). At Ryan Campground, blackbrush was the dominant shrub, with small trees of *Juniperus californica* and

Yucca brevifolia (= Mojave desert scrub, Turner 1982). The elevations of the two sites were 1372 and 1311 meters, respectively.

At both sites, *schusteri* was rare, with five of the six specimens caught when they were attracted to lights.

Tipula (Eremotipula) pellucida Doane

Tipula clara Doane 1901: 107–108 (preoccupied by *Tipula clara* Kirby 1884).

Tipula pellucida Doane 1912: 61, new name for *clara* Doane 1901: 107–108; Dietz 1921: 3, key; Alexander 1945a: 414, loc.; Alexander 1948: 29, loc.; Alexander 1949: 285, loc.; Alexander 1954: 39, loc.; Alexander 1965b: 38, cat.; Alexander 1967: 26, fig. 91 (male 9T, ID, apex of 8S), loc., key; Theischinger & Theowald 1981: 34, cat.; Teale 1984: 33, redesc., loc., key, biol.

Tipula pyramis Doane 1912: 53; Dietz 1921: 13, figs. 7, 7a (male 8S, lat., vent.) loc., key; Alexander 1948: 29, loc.; Alexander 1949: synonymy (but not stated as new synonymy); Byers 1976: 26–27, figs. 90–92 (male hypo., lat., dor.; 8S, apex), lectotype designation.

Diagnosis.—Wings light brown with the cells *c* and *sc* deeply yellowed; no pale streaks other than at cord (Fig. 443). *Male*: Apex of 8S with well developed membranous process covered with dense long setae on inner side (Fig. 201); membranous lobe between 8S and 9S elongate, acuminate and slightly sclerotized basally, apex nearly or completely reaching base of adminiculum (Fig. 199); ninth tergum with STP and dorsal lobes all short and broad (Fig. 185); OBL broad basally, curved laterally, and narrowing slightly to apex (Figs. 3, 191). *Female*: Thorax mostly brownish gray; abdomen with three dark stripes on tergites, the lateral pair grayish; each inner ridge of 8S low and pale, not or scarcely visible in lateral view; inner pigmentation areas of 8S mostly confluent medially.

Description.—*Length*: Male 16–20 mm; female 18–27 mm. *Head*: Vertex and postgena grayish brown and pruinose. Antennal length: male 4–5 mm; female 3–4 mm. *Thorax*: Males overall yellowish brown; females grayish brown, pruinose. Presutural scutum with faint stripes or stripes absent, darker in some females; median area between inner stripes brown or concolorous with remainder of thorax. Thoracic pleura mostly yellowish gray in males; grayish brown in females, with membranous areas contrastingly yellowish white. *Legs*: Femoral rings not evident in

males, faintly evident in females. *Wing*: Male 13–17 mm long, 3–5 mm wide; female 14–18 mm long, 3–4 mm wide. Overall light brown. Cells *c* and *sc* deeply yellowed, stripe along CuA less so, stigma only slightly darker (Fig. 443). Indistinct pale area surrounding stigma and extending as band along cord into discal, *m*₃ and *m*₄ cells. *Abdomen*: Terga 1–7 with medial and sublateral contiguous patches, forming longitudinal, nearly continuous grayish brown lines, contrasting with yellowish brown in males; patches of greatest extent in females, with abdomen often overall gray. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.4. Dorsal lobes short, strongly divergent, each broad basally, width nearly twice length, narrowing to subacute or rounded apex (Fig. 185). STP short, ratio of length STP/9T = 0.4, compressed, with slight, dorsal, longitudinal groove, width nearly equal throughout, apex gently rounded. Venter of process closed and pale, strongly reticulate to granulate (extending onto venter of 9T), with basal microtrichia (Fig. 188). Dark lateral flange connecting base of each dorsal lobe to STP, remainder of STP lightly sclerotized, dorsal margin smooth. Cuticle of ventral shelf areolate to reticulate (Fig. 187), margin entire. Ventral lobes strongly convergent (Fig. 186), mostly concealed, each lobe smooth, broad basally, narrowing slightly to broadly rounded apex. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of BS as in Fig. 195. Dorsolateral margin of BS greatly produced opposite posterior condyle of ID, apex of expansion with a small lobe, margin below lobe crenulate. No lobe near basistylar suture (Fig. 195). A9S without division into dorsal and ventral lobes; each ventral lobe without basal swelling and with long, scarcely thickened, erect, pale setae (Fig. 189). *Outer dististyle*: Posterodorsal margin slightly emarginate, anterior extension short to moderate in length (Fig. 190). *Inner dististyle*: Ventral surface of upper beak and dorsal surface of lower beak with strong ridges; apex of lower beak subacute to rounded. Crest small (Fig. 191); no scattered spinules, dorsal margin of crest serrulate. OBL of medium length, L/W = 2.1, dorsal margin curved strongly laterad (Figs. 3, 191), base of lobe broad. Lateral surface of OBL without ridge, medioventral margin expanded, apex broadly truncate or subacute (Figs. 192–194). *Adminiculum*: Lateral plates small, dorsal lobes short and rounded (Fig. 196). Wing-like expansions from near base of lateral plates extending dorsally

and anteriorly (Fig. 197); each lobe broad and usually with a short dorsal point, sometimes merely rounded (Fig. 198). Median lobe very small, exposed, with short recurved beak. *Eighth sternum*: Yellow longitudinal bands scarcely distinguishable. Posterior (sclerotized) margin slightly or moderately emarginate medially. Membranous apex strongly produced into a flat, tongue-like process (Fig. 201), outer surface of process membranous, inner surface lightly sclerotized with many dense setae (Fig. 199), length of setae nearly equal to that of lobe. Setae microscopically carinate, each carina with many sharp points (Fig. 200). Membranous lobe elongate, acuminate, apex of lobe reaching near base of adminiculum or even A9S (Fig. 199), about 2.6–3.2× as long as width at base; lobe lightly sclerotized at base, membranous near apex. Apical margin of 8S with a small, vestigial sclerite on either end, each sclerite with several setae. *Ovipositor*: Each inner ridge of 8S pale and relatively low throughout, not visible in lateral view in uncleared specimens (Figs. 202, 203). Membrane adjacent to anterior end of ridge expanded into distinct lobe, most developed as in Fig. 202. Outer pair of pigmentation areas small and often faint, inner pair of areas confluent medially along anterior two-thirds (Fig. 203). Vaginal apodeme elongate, expanded in width along middle half, abruptly narrowed along either end (Fig. 203).

Specimens examined.—*Type material*: *Tipula clara*. The type series as stated by Doane (1901) consisted of 4 syntypes: 2♂, 1♀, from Wawawai, Washington, and 1♀, Pullman, Washington. The type specimens of *Tipula clara* are all apparently lost, except for one wing mounted on a microscope slide and labeled "Type 166" (WSU). No specimens are included in the Doane types in the California Academy of Sciences, nor did I find any in the U. S. National Museum collection.

Tipula pyramis: Lectotype ♂ (designated by Byers 1976: 27; CAS # 5665): "Pyramid Lake/Nev. June 1911", "Coll. E. J./Newcomer", "R. W. Doane/Collection", "PROBABLE/PARATYPE/PYRAMIS", "Lectotype/Tipula/pyramis/R. W. Doane 1912/by G. W. Byers 1975". Condition of type series is described in Byers (1976: 26–27) and Arnaud (1979:37).

Other specimens: 211♂, 48♀. **USA: CALIFORNIA**: Lassen Co., Hallelujah Junction, 22-VI-1964, C. N. Slobodchikoff, 1♂, 1♀ (CAS); same but J. S. Glenn and B. E. Scott, 1♂, 3♀ (UCD); same but 9-VII-

1982, R. W. Brooks, 1♀ (UK); Modoc Co., Cedarville, (4770 ft), 29-V-1939, Aitken and Cazier; 5♂, 1♀ (USNM); Hackamore, 4-VI-1938, K. A. Salmon, 7♂, 1♀ (USNM); Nevada Co., Boca, 17-VI-1964, W. K. Thrailkill, 2♂ (UIM); Sagehen Creek, near Hobart Mills, 17-VI-1964, J. E. Slansky, 1♂, 1♀ (UCD) Plumas Co., Johnsville, 9-VI-1963, J. S. Buckett, 1♂, 1♀ (UCD). **COLORADO**: Mesa Co., 13 km S Mesa, 18-VI-1938, U. Lanham, 1♂ (UCM); Moffatt Co., Zenobia Peak, 6905 ft (2105m), 22-VI-1946, M. T. James, 1♂, 1♀ (USNM); Echo Point Overlook, Dinosaur National Monument, 8000ft (2438 m), 8-VII-1967, T. W. Davies, 1♂ (CAS). **IDAHO**: Ada Co., Boise, 23-V-1981, C. v. Nidek, 3♂ (ZMUA); Bear Lake Co., Bear Lake (about 42°3' N, 111°25'W), 6200 ft (1890 m), 9-VI-1920, no collector listed, 1♀ (AMNH); Butte Co., Craters of the Moon National Monument, 20-VI-15-VII-1965, D. S. Horning, Jr., 5♂, 5♀ (UIM); Camas Co., Willow Creek, 21 km NE Fairfield, 17-VI-1982, W. F. Barr, 7♂, 3♀ (UIM); Canyon Co., Parma, 2224 ft (678 m), 6-VI-1929, C. Wakeland, 1♂ (UIM); Cassia Co., City of Rocks, 1-VI-1979, D. B. Zeemar, 1♂ (USU); Elba, 13-VI-1960, B. A. Foote, 2♂ (UIM); Elba-Basin Pass, 22-VI-1959, W. F. Barr, 1♂, 1♀ (UIM); Elmore Co., Dixie, 10-VI-1960, B. A. Foote, 4♂ (UIM); Latah Co., Moscow, 2560 ft (780 m), 23-V-1931, P. Rice, 1♂ (UIM); Nez Perce Co., Lewiston Hill, 10-V-1924, A. L. Melander, 1♂ (USNM); Oneida Co., 8 km NW Holbrook, 8-VI-1972, G. F. Knowlton, W. J. Hanson, 3♂, 2♀ (USU); Holbrook Summit, 16-VI-1970, W. F. Barr, 3♂ (UIM); Rock Creek, 22-VI-1971, G. F. Knowlton, 1♀ (USU); Twin Falls Co., Lower Rock Creek Canyon, Sawtooth National Forest, 13-VI-1954, W. F. Barr, 4♂, 4♀ (UIM). **MONTANA**: Ravalli Co., mouth of Blodgett Canyon, 12-V-1969, C. B. Philip, 1♂ (USNM). **NEVADA**: Elko Co., Angel Creek Campground, 13 km SW Wells, 2134 m, 15-VI-1986, JKG #400, 1♀ (ANSP); Washoe Co., Reno, VI-1911, R.W. Doane Collection, 1♀ (CAS); White Pine Co., 9.8 km E of McGill, along Timber Creek, 2430 m, 14-VI-1986, JKG #399, 2♂ (JKG); county unknown, "Sheldon", on *Cercocarpus ledifolius*, 8-VII-1980, M. M. Furniss, 1♂ (UK). **OREGON**: Baker Co., Blue Mountains, Spring Creek, 3900 ft (1189 m), 30-V-1948 and 15-V-1949, J. Baker, 6♂, 1♀ (USNM); same county, specific locality unknown, 19-23-VI-1922, L. R. Dice, 2♂ (UMAA); same but 25-V-1961, J. Baker, 1♂, 1♀ (USNM); Deschutes Co., 32 km E Brothers, 19-VI-1967, R. M. Brown, 1♂ Hampton, 19-VI-1967, R. M. Brown, 1♂ (CAS); Grant Co.,

John Day Picture Gorge, 26-V-1950, K. Fender, 1 ♂ (USNM); Grant/Harney Co., Malheur National Forest, 12-VI-1947, K. Fender, 1 ♀ (USNM); Harney Co., Steens Mountains, Pike Cr., 23-V-1950, K. Fender, 3 ♂, 3 ♀ (USNM); same but Fish Lake, 7000 ft (2134 m), 11-VI-1927, H. A. Scullen, 1 ♂ (USNM); same but 11-VI-1961, J. Baker, 3 ♂, 3 ♀ (USNM); Harney Co., Stinking Water Mountain, 5000 ft (1524 m), 24-VI-1961, J. Baker, 1 ♂ (USNM); Klamath Co., Eagle Ridge, Klamath Lake, 20-V-1924, C. L. Fox, 1 ♂ (CAS); Klamath Falls, 12-V-1924, C. L. Fox, 1 ♂ (CAS); Lake Co., Paisley, 28-29-VI-1951, B. Malkin, 1 ♂ (USNM); Lakeview, 3-VI-1964, P. G. Gray, 2 ♀ (BYU); Malheur Co., Sucker Creek Canyon, 15-18-VI-1951, B. Malkin, 1 ♂ (USNM); county unknown, 3.2 km E of Bix, date unknown, K. Fender, 6 ♂, 1 ♀ (USNM). UTAH: Beaver Co., Mud Spring Ridge, 2.4 km E, 12.9 km N Manderfield, 2018 m, 11-VI-1986, JKG#393, 1 ♂, 1 ♀ (JKG); Box Elder Co., Honeyville, (1301 m), on raspberry, 27-V-1938, D. E. Hardy, 2 ♀ (USU); Golden Spike, 12-V-1979, C. R. Nelson, 1 ♂ (BYU); Big Hollow Creek, Raft River Mountains, 20-VI-1979, Baumann and Webb, 2 ♂, 1 ♀ (BYU); Long Birch Creek, near headwaters, 16-17-VII-1980, at light, R. Baumann and S. Clark, 5 ♂, 1 ♀ (BYU); Cache Co., Blacksmith Fork Canyon, 7-14-VII-1964, W. J. Hanson, Malaise trap, 2 ♂ (USU); Dry Canyon, Logan, 9-V-1938, G. S. Stains, 2 ♂ (BYU, USU); Green Canyon, near Logan, 5000 ft (1524 m), 9-VI-1959, G. Byers #3, 1 ♂, 7 ♀ (UK); same but 15-17-V-1972, R. W. Standage, 2 ♂ (USU); mouth of Greca (?) Canyon, 19-V-1922, R. Howell, 1 ♂, 1 ♀ (USU); Hyde Park, (1356 m), 2-VI-1942, G. F. Knowlton, 1 ♂ (USU); Logan, (1382 m), 2-VI-1938, at light, G. Knowlton, D. Hardy, 2 ♀ (BYU); same but 5-V-1943, G. Knowlton, 1 ♂ (USNM); same but VI-1956, at light, G. Knowlton, 3 ♂, 4 ♀ (UK); same but Utah State University, fields, 27-V-1973, J. Cameron, 1 ♂ (USU); Logan Canyon, 8-V-1938, D. Elmo Hardy, 1 ♂ (USU); same but 4800 ft (1463 m), 30-VI-1942, CPA, 2 ♂ (USNM); same but 1692 m, on *Lomatium triternatum*, 4-VI-1954, G. Bohart, 1 ♂ (UK); Menden, (1352 m), 27-V-1952, A. W. Buck, 1 ♂ (USNM); Sardine Canyon, 21-V-1938, D. Elmo Hardy, 4 ♂ (USU); Daggett Co., Elks Park, Ashley National Forest, 16-VI-1960, no collector listed, 1 ♂ (BYU); Juab Co., Eureka, (1949 m), 30-V-1-VII-1911, T. Spalding, 3 ♂ (ANSP); same but on *Cardaria draba*, 10-VI-1954, G. Bohart, 1 ♂ (UK); Trout Creek, Deep Creek Mountains, 27-VII-1982, Baumann and Cox, 1 ♀ (BYU); Kane Co., Kanab

Canyon, 5-V-1943, G. Knowlton, 1 ♂ (USNM); Milard Co., Maple Grove Forest Service Campground, Hwy. #50, S of Scipio, 6000 ft (1829 m), 13-VI-1976, G.W.B. #3, C. Young, 4 ♂, 12 ♀ (UK); same but 18-V-1989, P. Kitchen, 3 ♂, 1 ♀ (BYU); Oak Creek Campground, 5.3 km SE Oak City, 1798 m, 11-VI-1986, JKG #394, 1 ♂ (JKG); Oak Creek Canyon, 4-VI-1937, L. Jeppson, 1 ♀ (UCR); Rich Co., 19.1 km W Woodruff, on Utah Hwy. #39, 2256 m, JKG #406, 8 ♂, 5 ♀ (JKG); Laketown Canyon, 19-VI-1972, G. Knowlton, 2 ♂ (USNM); Monte Cristo, 21-VI-1956, G. Knowlton, 1 ♂ (UK); Salt Lake Co., Salt Lake City, 5000 ft (1524 m), 10-V-1954, G. Brooks, 1 ♂ (USNM); Sanpete Co., Fountain Green Spring, W of Fountain Green, (1827 m), 26-V-1978, R. Baumann, 3 ♂, 1 ♀ (BYU); Summit Co., Kamas, 11-VI-1956, G. Knowlton, 1 ♂, 2 ♀ (UK); Tooele Co., Stockton, (1545 m), 6-16-VI-1913, 16-VI-1914, T. Spalding, 3 ♂, 5 ♀ (ANSP, MCZ); Stansbury Mountains, Johnson Pass, (1901 m), 11-VI-1955, at light, H. E. Cott, 3 ♂, 1 ♀ (CAS); Little Valley Creek, Little Valley Campground, Sheeprock Mountains, 19-VI-1980, R. Baumann et al., 8 ♂, 1 ♀ (BYU); Utah Co., Crab Creek, near Thistle, 5-VI-1976, R. Baumann, 1 ♂ (BYU); Provo, (1387 m), 11-17-VI-1912, T. Spalding, 6 ♂, 3 ♀ (ANSP); Spanish Fork, (1387 m), 8-VI-1936, D. Hardy, 1 ♂, 1 ♀ (BYU); Spanish Fork Canyon, 6-VI-1975, no collector, 1 ♂ (BYU); Y Mountain, Sta. 7, 6-VI-1944, C. Lynn Hayward, 1 ♂ (BYU); Timpanogos Cave National Monument, 2-VI-1964, D. Huntzinger #1117, 1 ♂ (BYU); Wasatch Co., Weber-Provo Diversion, Hwy#189, below Francis, 29-VI-1982, R. Baumann and Sublette, 1 ♂ (BYU); Weber Co., Ogden, (1311 m), 5-VII-1942, G. Knowlton, 5 ♂ (USNM); same but 26-V-1971, R. Gerber, at light, 1 ♂ (USU); 8 km S Monte Cristo Forest Camp, 7500 ft (2286 m), 19-VI-1972, G. Knowlton, 1 ♂ (USNM); Eden, (1509 m), 4-VI-1938, G. Knowlton and G. Stains, 1 ♂ (USU); county unknown, Current Creek Valley, Uinta National Forest, 8000 ft (2438 m), 4-VII-1917, J. Silver, 1 ♀ (USNM); Cache Valley, O. Sacken, 1 ♂ (MCZ); Salt Lake, 6-7000 ft (1829-2134 m), 24-VI-1922, A. Lovett, 1 ♂ (USNM). WASHINGTON: Adams Co., Lind, (1365 ft), 5-IV, 6-V-1919, F. Carlson, A. Melander, 2 ♂ (UMAA, USNM); Benton Co., Hanford Works, 640 ft (195 m), 16-IV-1952, J. Davis, from sagebrush, 3 ♂ (UMAA, UK); Chelan Co., Wenatchee, (195 m), 19-IV, 4-V, A. Melander Coll., 17 ♂, 3 ♀ (USNM); Grant Co., Quincy, 30-V-1957, R. Abbott, 1 ♀ (UIM); Kittitas Co., Gingko State Park, 14-V-1948,

E. Ross, 1v (CAS); Klickitat Co., Maryhill, 28-IV-1938, K. Gray, in wild sunflower, 2♂ (USNM); Pacific Co., Nahcotta, no date or collector, 1♂ (UMAA); Spokane Co., Medical Lake, 9-V-1910, J. Hyslop, 1♂, 1♀ (USNM); Whitman Co., Almota, 20-V-1923, A. Melander, 3♂ (USNM); same but no date or collector, 1♀ (ANSP); Wawawai, (732 m), 20-V-1911, no collector, 1♂, 1♀ (ANSP, USNM); same but 30-V-1921, A. Melander, 1♂ (USNM); county unknown, Columbia River, 1-V, no collector, 1♂ (USNM). WYOMING: Carbon Co., Rawlins (about 41°47'N, 107°15'W), 6800 ft (2073 m), 26-VI-1920, collector unknown, 1♂ (AMNH); Teton Co., Grand Tetons, 9-VII-1942, CPA, 2♂ (USNM); same but Jenny Lake, String Lake and Hidden Falls, 6770–7000 ft (2063–2134 m), 1–7-VII-1941, CPA, 13♂, 1♀ (USNM); Grand Teton National Park, 23-VI-1956, T. Miura, 14♂, 4♀ (UK); Uinta Co., 23.5 km W Fort Bridger, on US Hwy#80, 2072m, 17-VI-1986, JKG#407, 2♂, 2♀ (JKG); county unknown, Bridge Basin, 7600 ft (2316 m), collector unknown, 1♂ (CMNH).

Discussion.—As noted above, the type series of *Tipula clara* (renamed *T. pellucida*) is largely lost. Fortunately, *pellucida* is a very distinctive species, and Doane's limited description (without illustrations) mentions the following diagnostic features: the nearly unicolorous wing with darker costal and subcostal cells ("... wings hyaline; costal and subcostal and the anterior margin of the anal cells and the stigma brown . . ."), a median, tongue-like process of the eighth sternum in the male ("... a medium rather broad projecting process the sides and rounded ends of which are furnished with long light yellow hair . . ."), and the placement of the species within the *impudica* group ("... hypopygium similar to that of *T. impudica* . . ."). He did not mention the elongate membranous lobe between the eighth and ninth sterna in the male, but this structure is not easily visible if the process of the eighth sternum is appressed to the ninth sternum. The slide-mounted wing agrees with Doane's description of the wing in *pellucida*.

I have found no other species of *Eremotipula* which is at all similar to *pellucida* in terms of wing coloration and male hypopygial characters and geographic distribution (e.g., *schusteri* and *enrystyla*, each with a much shorter median process of the eighth sternum, have streaked wings and are distributed in the Mojave Desert area). In addition, in 1924, A. L. Melander compared a specimen from Wenatchee, Washington, with the then

extant type specimens of *clara* and sent this to C. P. Alexander (CPA, taxonomic notes). I have examined both Alexander's sketches and a specimen agreeing with the above data (labeled "*Tipula clara* Doane", "A. L. Melander collection 1961"), and these agree with the description of *pellucida* by Doane and the redescription presented here.

I have examined the lectotype and paralectotypes of *Tipula pyramis* and confirm the synonymy of this species with *pellucida*, as first proposed by Alexander (1949). Dietz (1921) differentiated *pyramis* from *pellucida* in his key, stating that the process of the eighth sternum in *pyramis* is "elongate, pointed" while that of *pellucida* is "shorter, rounded". His illustration of *pyramis* does not show a "pointed" process. All specimens listed in his 1921 paper under *pyramis* have been examined by me and are clearly *pellucida*. One specimen in the Alexander collection, determined as *pyramis* by Dietz but not listed in his 1921 paper, is the unique holotype of *Tipula dissipina* described elsewhere in this paper.

Tipula pellucida shows more variation in the structure of the male genitalia than is found in most species of *Eremotipula*. This variation does not appear fixed in any populations nor correlated with other characters, however, so does not indicate subspecific or specific status for the variant populations. The apex of the outer basal lobe is highly variable, from boot-shaped in most specimens to broadly truncate in specimens from Washington and elsewhere (Figs. 192–194), notched slightly in others, and subacute in some specimens from Utah. The margin of the wing-like expansions of the adminiculum also varies, often rounded in specimens from California, Washington and elsewhere (Fig. 198) instead of with a short point (Fig. 197). The curvature and length of the membranous lobe vary even within a population, the lobe in some individuals straight and not quite reaching the adminicular base, in others, curved apically and nearly reaching the appendages of the ninth sternum. Finally some variation in the lateral margin of the basistyle, opposite the posterior condyle of the ID, was noted.

The illustrations of Alexander (1967: fig. 91) of the male genitalia in *pellucida* show a combination of both dorsal and ventral aspects of the ninth tergum, and a ventromesal view of the inner dististyle.

Tipula pellucida is extremely easy to recognize in the male sex, and the female can only be confused with a few other species, using characters in the key. In females, the extensively gray thorax and abdomen, with contrasting yellowish brown, and the broad dorsolateral gray stripes (often abdomen mostly gray overall), combined with the wing coloration, is useful for determination and may be all that can be observed in pinned specimens without relaxing and clearing the genitalia. The low pale ridges of the 8S and raised adjacent membranous area (forming a lobe) can sometimes be observed in pinned specimens. For cleared female genitalia, the pigmentation pattern of the eighth sternum is unique among the known species.

Relationships.—*Tipula pellucida* possesses an extraordinary number of autapomorphies in male genitalic features, and it is this highly modified nature of the male characters that obscures the homologies which could clearly determine its evolutionary relationships to other species of *Eremotipula*. The final phylogenetic analysis places *pellucida* in several equally parsimonious positions within the derived species groups (Figs. 21, 31, 32). It also may be a sister species to *schusteri*, as both species have a median apical process on the eighth sternum.

Geographic distribution.—Western Colorado westward to northeastern California, northward to Washington and Montana (Fig. 204).

Seasonal distribution.—Flight records range from April 5 to July 17, with most in May and June. Earliest records were from central Washington at low elevations, the later summer records from higher elevations throughout the range of the species. Several August collection records are cited in the literature (Dietz 1921; Alexander 1948) but could not be verified.

At Logan, Utah, where *pellucida* has been commonly collected, specimens were secured from May 5 to June 2, varying with the year. Within Cache Co. (including Logan), an area encompassing a wide range of elevations and exposures, adults could be found as late as June 30.

Habitat.—There is little in the literature regarding habitats of *pellucida*, even though this species is widespread and often collected. Alexander (1945a: 414) collected *pellucida* among lodgepole pines (*Pinus contorta*) in Grand Teton National Park, Wyoming, and Teale (1984: 34) described habitats at two sites based on field col-

lections by G. W. Byers. In northern Utah, Byers collected *pellucida* on sagebrush (*Artemisia*), while in central Utah, he found *pellucida* in a mostly deciduous woodland dominated by various *Acer* species, with undergrowth of barberry, rose and *Salix* sp. Of the five sites in Nevada, Utah and Wyoming where I have collected this species, the vegetation of all but one (Millard Co., Utah) was dominated by *Artemisia tridentata* shrubs with scattered taller vegetation of *Juniperus* spp., *Amenanchier utahensis* or *Cercocarpus* sp. At the Millard Co. site, I collected *pellucida* on canyon slopes with patches of *Quercus* and *Artemisia tridentata*, and scattered pinyon pines. At one site (Rich Co., Utah) pupal skins, probably of this species, were found on the soil near or under *Artemisia* shrubs; otherwise the immatures are unknown.

Coincident with its broad geographic range, *pellucida* can be found from 194 m (640 ft) in central Washington to over 2000 m (6800–8000 ft) in Nevada, Wyoming and elsewhere. One collection at 3046 m (10,000 ft) in the Raft River Mountains, Utah is exceptional (cited in Alexander 1948, but specimen not seen by me).

I found *pellucida* uncommon at all sites where I encountered it, although Alexander (1945a) states that this species was "the commonest crane-fly among the lodgepole pines" in the Teton Mountains, and C. R. Nelson (pers. comm.) found it in "enormous numbers" on the slopes of a mountain pass in Box Elder Co., Utah.

The madina Species Group

This species group includes *byersi*, *impudica*, *jicarilla*, *madina* and *spaldingi*. The synapomorphies of these five species are given in Fig. 21 with alternative resolutions of relationships explained in the discussion (Figs. 22, 25–28).

Tipula (Eremotipula) jicarilla, new species

Diagnosis.—Wing light brown with strongly yellowed *c* and *sc* cells; no pale streaking other than stigma. **Male:** 9T with relatively short pointed dorsal lobes (Fig. 206), ventral plate without distinct lobe (Fig. 207), outer basal lobe of ID flattened with nearly acute apex (Fig. 210), lack of basistylar lobe or spine (Fig. 205), emarginate border of adminiculum (Fig. 209), 8S with short rounded membranous lobe. **Female:** Inner ridges of 8S moderately long and pale (Figs. 211–213). Distributed in central New Mexico.

Description.—*Length*: Male 14–15 mm, female 18–23 mm. *Head*: Vertex and postgena brownish gray, with orangish or yellowish patches sublaterally on occiput. Antennal length: male 4–5 mm, female 2–3 mm. *Thorax*: Overall light brownish gray, pruinose. Presutural scutum with two pairs of brown lines, inner pair narrow and not strongly delimited; lateral pair broad. *Legs*: Femoral rings absent in males, light to dark brown in females. *Wing*: Male 14–15 mm long, 3–4 mm wide; female 15–18 mm long, 3–4 mm wide. Overall light brown; stigma scarcely darker. Cells *c* and *sc* strongly yellowed. Pale area surrounding stigma, extending as band along cord through discal cell and into proximal sections of cells *m*₃ and *m*₄. *Abdomen*: Terga 2–6 usually with sublateral and dorsal brown patches, markings faint dorsally; nearly contiguous laterally with extreme lateral border of tergites pale, bordering brown patches. *Hypopygium*: *Ninth tergum*: Dorsal lobes subparallel, each small, triangular, with apex acute, slightly downturned (Fig. 206). STP elongate, strongly compressed, with abruptly narrowed, pale apex and dorsal margin slightly lacinate. Cuticle of STP not reticulate. Ventral lobes partially concealed beneath dorsal lobes, slightly convergent (Fig. 207); each smooth, broad, flat, with rounded margin. Ventral surface and margin of ventral plate smooth. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of basistyle opposite attachment site of *sp*1 slightly expanded. Dorsolateral margin of BS only slightly produced opposite posterior condyle of ID (Fig. 205). Ventral lobe of A9S mostly membranous, with short, thickened, reddish brown setae restricted to dorsal edge (Fig. 208); lobe partially concealed. *Outer dististyle*: Posterodorsal margin straight, anterior extension of moderate length (Fig. 205). *Inner dististyle*: Ventral surface of upper beak with well-developed ridges, those of lower beak obsolete. Crest pale (Fig. 210), developed anteriorly along lateral surface of upper beak, with groove between crest and dorsum of upper beak usually equal to half width of lower beak. Dorsal margin of crest nearly straight, serrulate, nearly reaching outer basal lobe posteriorly, scattered spinules on crest. OBL large, directed posteriorly and slightly bent laterally along posterior half, lateral surface mostly smooth, apex strongly narrowed. *Adminiculum*: Lateral plates expanded basally, abruptly narrowed beyond dorsal spine (Fig. 209) with margin rounded. Dorsal lobes narrow, fused basally, apices separated,

rounded, without striae. Median lobe small (Fig. 208), beak distinct; without lateral carinae, posterior margin dark. *Eighth sternum*: No yellow bands. Posterior (sclerotized) margin slightly produced medially (rounded). Membranous apical region with band of long setae, denser toward the middle; band interrupted medially. Setae over half as long as eighth sternum, with numerous, rounded carinae; no lateral setae distinctly thickened or lengthened (Fig. 205). Membranous lobe short, broad and rounded, about as long as wide, with single (ungrouped) microtrichia on tubercles. *Ovipositor*: 8T yellowish brown, posterior margin slightly concave. 9T reddish-brown, sometimes shiny. 10T reddish-brown, shiny, more or less swollen posteriorly. Longitudinal apodeme well developed, not strongly narrowed anteriorly. Cerci elongate, slightly to moderately upturned apically, yellowish brown. 8S light brown proximally, remainder yellowish brown, often darker brown or reddish brown medially (Figs. 211, 212). Hypogynial valves light reddish brown, apices narrowly rounded (Fig. 213). Inner ridges of 8S each moderately long, low, pale (Figs. 212, 213); pigmentation light brown, reaching to posterior end of ridge only laterally.

Specimens examined.—*Type material*: Holotype ♂ (ANSP): NEW MEXICO: Lincoln Co., Jicarilla Mtns., nr Jicarilla, T5N,R12E,23, 27-V-1991, at light, J. Gelhaus #508, C. Nelson. Paratypes: 3♂, 6♀. NEW MEXICO: Bernalillo Co., Sandia Mountains, Sunset Canyon, Albuquerque, 1920 m, 23-V-1979, JKG #1, 1♀ (ANSP); Lincoln Co., topotypic, 2♂, 4♀ (ANSP, USNM); Sacramento Mtns., Philadelphia Canyon, 3.2 km W Angus, T10S, R13E, 8, elev. ~2000m; 29-V-1991, from shaded rock crevice, JKG #510, C. Nelson, 1♂ (ANSP); Sandoval Co., Sandia Mountains, 8.5km (5.3 mi) SSE Placitas, elev. 1981m, 15-VI-1979, GWB #5, 2♀ (UK).

Etymology.—This species is named for the Jicarilla Apache Indian tribe, for which the type locality derives its name. The species epithet is a noun in apposition.

Discussion.—The female of *jicarilla* is difficult to distinguish from that of *impudica*, and the two species may be found to have slightly overlapping distributions in northern New Mexico. As stressed in the key, the wing pattern is best used for distinguishing the two species, particularly the lack of streaking in the anal cell of *jicarilla*. The female genitalic morphology of the two species is

extremely similar and I know of no reliable distinctions.

Relationships.—This species is placed as the sister species to the other species in the *madina* group in the phylogenetic analyses, or as a sister species to *byersi*.

Geographic distribution.—Central New Mexico (Fig. 297).

Seasonal distribution.—May 23 to June 15.

Habitat.—*Tipula jicarilla* has been collected at the Lincoln Co. sites in habitat dominated by *Pinus ponderosa*, pinyon pine (*Pinus* sp.), alligator juniper (*Juniperus deppeana*), with an understory of scrubby oaks (*Quercus* sp.). The specimens from the Sandia Mountains were collected on slopes with vegetation typical of Great Basin conifer woodland (Brown, 1982a), including dominants of *Juniperus* sp. and *Cercocarpus* sp. with understory shrubs of *Cowania mexicana*, *Chrysothamnus* sp., *Atriplex* sp., and also *Opuntia* spp. and various grasses and herbaceous annuals. The few specimens collected have been taken at around 2000 m.

Tipula (Eremotipula) byersi, new species

Tipula spaldingi: Alexander 1948: 30, figs. 9 (9T, ID, OD, adm., 8S), redesc., loc.

Diagnosis.—*Male*: hypopygium as in *madina* species group with outer basal lobe of ID broad and mostly smooth on lateral surface (Fig. 217); crest of ID well-developed anteriorly, with wide groove between crest and upper beak but distinguished by large ventral lobe of A9S (nearly equal in size to dorsal lobe, Fig. 216) with dorsal protuberance, dorsal lobes of adminiculum bifurcated and spinous (Fig. 220), eighth sternum with single row of thicker setae and medial patch of fine setae (Fig. 223). *Female*: unknown.

Description.—*Male*: *Length*: Male 19 mm. *Head*: Vertex and postgena yellowish brown to brownish gray. Antennal length: male 4–6 mm. *Thorax*: Overall yellowish brown to brown, pruinose. Presutural scutum with two pairs of indistinct, reddish brown to brown lines. *Legs*: Femoral rings brown, distinct. Tibiae with darkened apices. *Wing*: Male 16–17 mm long, 4 mm wide. Overall light brown; stigma brown. End of Sc darkened. Pale area surrounding stigma and extending as pale band along cord into cell m_3 ; broad, indistinct, pale patch near midlength of cell m extending across cell cu and along A_1 to

wing margin. *Abdomen*: Sublateral brown markings absent on most terga, only faintly evident on 2 and 3. Marginal setae of tergum 1 long and dark, about 3x length of preceding setae (equal to ventral setae). *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5. Dorsal lobes subparallel to slightly divergent (Fig. 214), each subtriangular, elongate, slightly longer than width at base, apex acute and slightly downturned; medial margin minutely toothed. STP elongate, ratio of length STP/9T = 0.6, compressed, apex abruptly narrowed and pale, with dorsal margin slightly lacinate. Cuticle of STP not reticulate. Ventral lobes partially concealed beneath dorsal lobes, subparallel (Fig. 215); each smooth, flat, with narrowly rounded apex (faint ventral ridge in paratype). Ventral surface and margin of ventral plate smooth. *Ninth sternum* (+ *basistyle*): Dorso-medial margin of basistyle slightly produced opposite attachment of sp1. Dorsolateral margin of BS opposite posterior condyle of ID with a short, thick, apical point (Fig. 219). Ventral lobe of A9S large (Fig. 216), with strongly sclerotized, dorsal knob and with short, thickened, blunt-tipped, reddish brown setae. *Outer dististyle*: Posterodorsal margin straight, anterior extension of moderate length. *Inner dististyle*: Ventral surface of upper beak and apex of lower beak with well-developed ridges. Crest pale (Fig. 217), developed anteriorly along lateral surface of upper beak, with groove between crest and dorsum of upper beak equal to width of lower beak; spinules scattered near the base. Dorsal margin of crest slightly convex or concave, serrulate, reaching OBL posteriorly. OBL large, broad, L/W = 1.3–1.7, directed posteriorly and slightly bent laterally along posterior half, lateral surface smooth, apex rounded. *Adminiculum*: Lateral plates greatly expanded (Fig. 220), a small transverse carina on each plate anteriorly near base with two small teeth dorsally near lateral edge, an elongate, inwardly-curved spine more mesally (Fig. 221). Dorsal lobes completely separate between median lobe and dorsal spines, each lobe with apex bifurcate, inner spine-like tip elongate. Median lobe compressed (Fig. 222), with long beak. *Eighth sternum*: Yellow bands obsolete. Posterior (sclerotized) margin bi-concave. Membranous apical region with single row of long, smooth setae, a large medial patch of finer setae, almost reaching membranous lobe (Fig. 223); no distinct lateral sclerites. Setae nearly as long as eighth sternum; only medial, fine setae with

rounded microscopic carinae, all setae with granulate surface at 400x. Membranous lobe minute, rounded, with single (ungrouped), thickened microtrichia.

Specimens examined.—*Type material*: Holotype ♂ (UK): ARIZONA: Coconino Co., Double Springs camp, west side of Lake Mormon, 7140 ft (2176 m), 11 June 1979, George W. Byers #5. The genitalia have been cleared and placed in glycerin in a genitalia vial attached to the pin of holotype. Paratype: UTAH: Washington Co. (probably), Zion National Park, no date, B. E. Rees #18335, det. *Tipula spaldingi* Dietz by C. P. Alexander, 1946, 1♂ (USNM). The left wing and the genitalia were mounted by Alexander on a microscope slide similarly labeled as the pinned specimen.

Etymology.—I name this species for Dr. George W. Byers, whose outstanding research and advice concerning crane fly systematics has been a great influence in my own work.

Discussion.—Alexander (1948: 30) redescribed what he thought was *spaldingi*, but apparently he never examined the types of *spaldingi* and instead relied on Dietz's poor description and illustration. Unfortunately, he based his redescription on two specimens that were not *spaldingi* but a male of *byersi* and a male of *kaibabensis*. Both specimens were found in Alexander's synoptic collection determined as *spaldingi* and were re-examined during this study. The description and illustrations of the hypopygium of *spaldingi* by Alexander clearly refer to the slide-mounted hypopygium of the male of *byersi*. Although the redescription is reasonably accurate for the specimen, the figure of the mesal view of the inner dististyle (drawn from the slide) is misleading. The crest is described as "small"; in fact, on the slide, the crest is large and well-developed anteriorly along the lateral surface of the upper beak, and the dorsal margin is serrulate. The "gonopophyses" described by Alexander refer to the dorsal lobes of the adminiculum.

Males of *byersi* can be distinguished from other species in the *madina* group (*impudica*, *madina* and *spaldingi*) by the characters listed in the key and diagnosis. Not easily visible on the adminiculum, but also diagnostic, is the compressed median lobe with a prominent beak. In addition, the range of *byersi* is widely separated from that of *spaldingi* and *impudica*, and probably only narrowly overlaps that of *madina* in southern Utah.

Relationships.—The large ventral lobe of the appendage of the ninth sternum in *byersi* and *im-*

putica appears to indicate a close relationship of the two species, but is conflicted by other characters as noted in the phylogenetic analyses. Evidence for a sister species relationship between *byersi* and *spaldingi* is not strong, although both have elongate outer dististyles and basistylar spines.

Geographic distribution.—Central Arizona to southern Utah (Fig. 224).

Seasonal distribution.—June.

Habitat.—The type locality is near the Mogollon Rim in a primarily closed-canopy forest of ponderosa pine, with smaller Gambel oak and scattered grasses. This site is unusual as it lacks the open woodland or shrubland which is commonly used by most other species of *Eremotipula*.

Tipula (*Eremotipula*) *impudica* Doane

Tipula impudica Doane 1901: 104; Dietz 1921: 13, figs. 6, 6a-c (hypo., dor., lat.; 9T, dor., vent.), key, loc.; Alexander 1949: 284, loc.; Alexander 1954: 38, loc.; Alexander 1965a: 340, fig. 8 (OD, ID); Alexander 1965b: 36, cat.; Alexander 1967: 25, key; Byers 1976: 21, discussion of types; Theischinger & Theowald 1981: 22, cat.; Teale 1984: 31–32, redesc., loc., key.

Tipula albocincta Doane 1901: 110; Alexander 1965b: 35, cat.; Theischinger & Theowald 1981: 6, cat.; Teale 1984: 31–32, discussion of type. **NEW SYNONYMY.**

Diagnosis.—Wings with white areas at cord and along A_1 , cells *c* and *sc* yellowed. *Male*: hypopygium as in *madina* group (outer basal lobe of ID broad and mostly smooth on lateral surface and crest of inner dististyle well-developed anteriorly (Fig. 227), with wide groove between crest and upper beak), distinguished by large, protruded ventral lobe of A9S with short, thickened setae (Fig. 239); dorsal lobes of 9T with apices subtruncate, lobes often short (Figs. 234, 237). *Female*: Low, pale inner ridge of 8S (Fig. 245).

Description.—*Length*: Male 14–19 mm; female 16–24 mm. *Head*: Vertex and postgena yellowish brown to brown, heavily pruinose. Antennal length: male 4–5 mm, female 3 mm. *Thorax*: Overall yellowish brown to brown, heavily pruinose. Presutural scutum with two pairs of indistinct to distinct, reddish to dark brown stripes; medial area between stripes often without pruinosity, but with a thin dark line bisecting notum. *Legs*: Femoral rings brown, sometimes indistinct. *Wing*: Male 14–18 mm long, 3–4 mm wide; female 14–18 mm long, 3–5 mm wide. Overall light brown; stigma brown. Cells *c* and *sc* yellowed, usually

strongly so, contrasting with light brown coloration of most of rest of wing. Pale area nearly surrounding stigma and extending as band along cord into proximal sections of cells m_3 and m_4 . Pale streak along middle section of A_1 . *Abdomen*: Terga 2–8 with nearly contiguous dorsal and sublateral brown patches. *Hypopygium*: *Ninth tergum*: Ratio of length $9T/BS = 0.5–0.6$. Dorsal lobes subparallel to slightly divergent (Fig. 234), each short to extended, $0.5–1.5\times$ as long as wide, only slightly narrowing apically, apex variable, usually truncate but lateral edge often produced into an acute lateral point (237, 238). STP elongate, ratio of length $STP/9T = 0.5–0.7$, compressed, with strong dorsal ridge extending entire length (nearly triangular in cross section), apical fifth pale and narrowed with dorsal margin smooth to slightly laciniate. Cuticle of STP not reticulate. Ventral lobes partially concealed beneath dorsal lobes, slightly convergent (Fig. 235); each short, narrow to broad, smooth, apex usually concave (Figs. 237, 238), lobe extending from broad flat plate. Ventral surface of plate smooth. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of basistyle usually not produced opposite attachment of $sp1$ (Fig. 226), sometimes with a short projection. Dorsolateral margin of basistyle opposite posterior condyle of inner dististyle produced slightly into flat lobe (Fig. 225), margin usually smooth and rounded, sometimes with a short spine. Ventral lobes of $A9S$ large (Fig. 239), subquadrate and protruding, with short, thickened, laterally-directed setae. *Outer dististyle*: Posterodorsal margin shallowly concave, anterior extension short (Fig. 228). *Inner dististyle*: Ventral surface of upper beak and apex of lower beak with well-developed ridges. Crest pale (Fig. 227), developed anteriorly along lateral surface of upper beak, with groove between crest and dorsum of beak greater than width of lower beak; scattered spinules along the base. Dorsal margin of crest slightly to moderately concave, serrulate to deeply laciniate; usually reaching OBL posteriorly. OBL large, $L/W = 1.5–1.7$, directed posteriorly, dorsal margin slightly bent laterally in posterior half, lateral surface nearly smooth and flat, without ridges but sometimes slightly wrinkled near dorsal margin, apex narrowed and subacute. *Adminiculum*: Lateral plates expanded throughout, fused with dorsal lobes (Fig. 229), lateral margin irregular, roughened area at base. Dorsal lobes completely separated between median lobe and dorsal spine (Fig. 231), each lobe mostly flat,

smooth, with inner edge upturned against median lobe, with 1–3 acute points dorsally (Figs. 229, 232, 233), ending posteriorly in spine, lobe sometimes also expanded ventrally. Median lobe large, height about half of total adminiculum, thickened, with slight carina along posterior margin on either side (Figs. 229, 230), ventral margin roughened, with irregular line extending dorsally; a pair of well-developed, dorsoventral ridges below median lobe on either side of posterior margin. *Eighth sternum*: Posterior (sclerotized) margin shallowly concave (Fig. 240). Membranous apical region with band of setae, mostly 2–3 setae wide but broadened at middle (Fig. 241); a small sclerite with several setae at either end of band (Fig. 241). Setae without carinae; length about half of sternum. Membranous lobe minute (Fig. 242), with short, single, mostly blunt spicules. Membranous region bordering lobe tuberculate, with singly spaced microtrichia; rarely with light sclerotization around lobe. *Ovipositor*: 8T and 9T mostly brown to darker brown, 9T sometimes partly shiny. 10T yellowish to reddish-brown, shiny, scarcely or not swollen posteriorly, sometimes slightly darkened posterolaterally. Cerci moderate length, about length of 10T, slender, light reddish brown (often darker basally), only slightly upturned apically. 8S brown and pruinose basally, remainder pale and shiny, with reddish brown medially. Hypogynial valve blades with apices narrow to broadly rounded (Fig. 245). Inner ridge of 8S moderately developed, low, pale (Fig. 245); pigmentation faint along inner grooves, outer pigmentation light brown, usually only reaching to posterior end of ridge.

Specimens examined.—*Type material*: *Tipula impudica* Doane. Lectotype ♂ (designated here, WSU): The specimen is labeled “Wawawai/5–11–98 Wash”; “Collector/R.W.Doane”; “Type/159” (handwritten in red ink); a blank red square card; and my lectotype label. Doane (1901: 104) described *impudica* based on 2♂ from Wawawai, 2♂ from Almota and 1♂, 1♀ from Pullman (all Whitman Co., Washington). The word “Type” was inserted after the listing of the Wawawai specimens, but no reference was made to either specimen specifically. According to Byers (1976), “Doane usually in some way labeled only one (specimen) as ‘type’ . . .”, and in the case here, a male from Wawawai at WSU is uniquely labeled. In keeping with Doane’s labeling, I choose this male as the lectotype for *impudica*; to stabilize the

concept of this species name. The left wing has been removed (presumably by Doane) and mounted on a microscope slide labeled "Type 159". The lectotype lacks all legs except two that are glued to the red paper square.

Paralectotypes: All WASHINGTON: Whitman Co.: 2♂, Almota, 20-IV-1890, C. V. Piper (CAS, WSU); 1♂, topotypic, 7-V-1898, R. W. Doane (USNM); 1♂, 1♀, Pullman, no date, R. W. Doane Collection (CAS). An additional male from Pullman (ANSP) and a female from Wawawai (USNM), although labeled as types, are not among those listed in the original description.

Tipula albocincta Doane. Holotype ♂ (USNM): The specimen is labeled: "Colo."; "Type no. 10938/U.S.N.M." (red label); "Type 171" (handwritten in red ink); "Tipula/albocincta/Doane". The holotype lacks all legs, but is otherwise in good condition.

Other specimens: 216♂, 57♀. **CANADA:** ALBERTA: Blakemore, 16-VI-1989, C. & A. v. Nidek, 1♂ (ZMUA); Keremeos, 7-9-V-1923, P. N. Vroom, 5♂ (USNM); Oliver, (ca. 305 m), 4-30-V-1923, C. B. D. Garrett, 63♂, 3♀ (UMAA, USNM). **USA:** COLORADO: Alamosa Co., Mosca Pass Trail, 8900 ft (2713 m), 28-IV-1984, H. A. Harding, 1♂ (UK); Boulder Co., Boulder, (1631 m), 27-IV-1924, S. A. Rohwer, 3♂, 1♀ (USNM); same but 28-V to 3-VI-1926, M. C. Van Duzee, 5♂, 1♀ (CAS); same but 1-VI-1938, at light, U. N. Lanham, 2♂ (UCM); same but 10-VI-1944, C. Combs, 1♂ (UCM); same but 3-VI-1932, M. James, 1♀ (USNM); same but 5-VI-1934, H. Rodeck, 1♀ (UCM); 2 mi N Jamestown, 2195 m, 1-VII-1982, U. Lanham & J. Graham, 1♀ (UCM); Jim Creek, 21-VI-1922, 1950m, 1♀ (AMNH); Clear Creek Co., Clear Creek Canyon, 11-VII to 17-VIII, 1912, 18-VI-1913, 10-VI-1923, Oslar, 10♂, 3♀ (UMAA, ANSP); Doolittle Ranch, Mt. Evans, 9800 ft (2987 m), 1-VIII-1961, C. H. Mann, 1♂ (specimen not examined); Eagle Co., State Bridge, near Bond, 7000 ft (2134 m), 24-25-VI-1961, B. H. Poole, 2♂ (specimens not examined); El Paso Co., Manitou, (1958 m), 20-23-VI-1926, E. C. Van Dyke, 1♂, 1♀ (CAS); North Cheyenne Canyon, 27-VI-1934, CPA, 1♂ (USNM); Palmer Lake, (2202 m), 5-7-IX-1917, Oslar, 2♂ (ANSP); Garfield Co., Cardiff, "31-VI" to 12-VII, 1918, Oslar, 11♂ (ANSP); Glenwood Springs, (1751 m), 27-29-VI-1918, Oslar, 4♂ (ANSP); New Castle, (1692 m), 15-16-VII-1918, Oslar, 3♂, 2♀ (ANSP); Huerfano Co., Dog Springs Arroyo, 18-VI-1962, P. Robinson, 1♂ (UCM); Jack-

son Co., North Park, VII-1922, Oslar, 1♂ (UMAA); Jefferson Co., Bear Creek, Morrison, (1768 m), 12-VI-1914, Oslar, 3♂ (ANSP); Red Rocks Park, Morrison, 16-VI-1933, H. Gibbons, 1♀ (UCM); Chimney Gulch, Golden, (1729 m), 22-29-VI-1912, 5-15-VI-1914, 15-VI-1919, Oslar?, 21♂, 17♀ (ANSP, UK); Leyden, VII, Oslar, 1♂ (UMAA); Jefferson/Douglas Cos., Platte Canyon, 25-V-1901, Dyar & Caudell, 4♀ (USNM); Larimer Co., Estes Park, 2292 m, Oslar, 1♂, 1♀ (ANSP); Las Animas Co., Raton Pass, (2388 m), 15-VI-1947, CPA, 1♂ (USNM); Mesa Co., 31 mi N Mack, 25-VII-1975, A. Menke & W. Pulawski, 1♀ (USNM); Montezuma Co., Mancos, (2131 m), 10-VIII-1918, Oslar, 2♂ (ANSP); Park Co., Kenosha Pass, (3048 m), VII, Oslar, 4♂ (UMAA); Webster, 23-VI-1916, (2746m) Oslar, 2♂ (ANSP); Garfield Co., Four Mile Creek, 7-17-VII-1918, Oslar, 3♂, 2♀ (ANSP); ? Co., Halls Valley, 23-VI-1916, Oslar, 1♂ (ANSP); Slate Cr., 10-VII-1929, Clagg, 1♂ (USNM); no locality information, 26♂, 17♀ (ANSP). **IDAHO:** Nez Perce Co., Lewiston Hill, 10-V-1924, 3-V-1925, A. L. Melander, 7♂ (USNM). **MONTANA:** Park Co., Eagle Creek Road, 3 mi NE Gardiner, 1890 m, 21-VII-1964, H. B. Leech, 1♀ (CAS); Ravalli Co., Woodside, 21-V, Ashburn & Stiles, 1♂ (USNM). **NEW MEXICO:** Colfax Co., Sugarite Canyon, 1.5 mi S Lake Malloya, 2255m, 17-VI-1979, GWB #10, 1♀ (UK). **OREGON:** Deschutes Co., Deschutes River near Redmond, (912 m), 27-V-1950, K. Fender, 2♂, 1♀ (USNM); Grant Co., John Day Picture Gorge, 26-V-1950, K. Fender, 2♂, 1♀ (USNM); Malheur Co., Juntura, 26-V-1948, J. E. Davis, 1♂ (USNM). **UTAH:** Duchesne Co., Uintah Canyon Campground, 25.8 km NW Neola, 2316 m, 13-VII-1985, at light, JKG #314, 1♂ (JKG). **WASHINGTON:** Adams Co., Lind, (413 m), 5-IV-1919, A. L. Melander, 2♂ (USNM); Asotin Co., Asotin (235 m), 16-V-1923, A. L. Melander, 1♂ (USNM); Asotin Creek, 27-IV-1924, A. L. Melander, 7♂ (USNM); Douglas Co., Columbia River, 1-V-1919, A. L. Melander, 1♂ (USNM); Kittitas Co., Vantage, 26-IV-1935, J.I.M., 1♂, 1♀ (USNM); Whitman Co., topotypic, (731 m), 15-V-1921, 28-V-1922, A. L. Melander, 8♂ (USNM). **WYOMING:** Albany Co., Pole Mountain, ca. 16 km SE Laramie, (2651 m), 30-VII-1950, D. G. Denning, 1♂ (UWL); Rogers Canyon, 8 & 9.5 mi NE Laramie, 6-VII-1981, at U.V. light, coll. unknown, 15♂, 7♀ (UWL); Albany/Platte Cos., Sybille Canyon, 28-V-1981, collector?, 10♂, 1♀ (UWL); Carbon Co., Bottle Creek Campground, 7 mi SW Encampment, 4-

VIII-1967, 2682 m, F., P. & M. Rindge, 1 ♀ (AMNH); Hot Springs Co., 2.3 mi SW Thermopolis, Route 120, 24-VI-1980, at light, M. Pogue, R. Lavigne, 1 ♀ (UWL); Park Co., no specific locality, 13-VII-1950, at light, GWB, 1 ♀ (UMAA); Platte Co., Glendo, (1439 m), 10-VI-1960, 1-VI-1961, 16-V-1962, R. J. Lavigne, 3 ♂ (USNM); Platte Co., 15-VI-1951, R. E. Pfadt, 1 ♂ (UWL).

Discussion.—*Tipula impudica* and *albocincta* were described simultaneously, and although the descriptions are similar, Doane made no comparison of the two species. The type of *albocincta* is conspecific with that of *impudica*, both exhibiting a large ventral lobe on the appendage of the male ninth sternum, a well-developed crest of the inner dististyle, a minute membranous lobe of the eighth sternum and other similarities. *Tipula impudica* has strict page priority, but, more importantly, *impudica* has been recognized subsequent to the original description, while *albocincta* has not.

Tipula impudica shows great variation in the size and apical margin of the dorsal (Figs. 234, 236–238) and ventral (Figs. 235, 237–238) lobes of the male ninth tergum, the number of spines on the dorsal lobes of the adminiculum (Figs. 229, 232, 233), as well as the development of the basistylar margin. The only variation showing geographic restriction is that of the dorsolateral margin of the basistyle. This margin may be produced into a short spine (similar to that in *spaldingi* and *byersi*, Fig. 257), or the spine scarcely developed, or with the margin smooth. Although all conditions occur among specimens from Colorado and Wyoming, individuals with spines greatly predominate in these areas, and no individuals are seen with spines outside this region.

Females are difficult to separate from other members of the species group but can be identified by the characters in the key, particularly the low pale inner ridge of the 8S and the wing patterning: *spaldingi* has much more contrastingly patterned wings and the ridge is high; *madina* lacks pale areas along vein A₁ and in cell m₄, and cells c and sc are not yellowed; *jicarilla* females lack a pale streak in cell a₁.

Relationships.—Possible sister species relationships of *Tipula impudica* are given in the phylogenetic analysis. Although *impudica* does appear to be most closely related to *madina* and *spaldingi*, due to the toothed dorsal lobes and thickened me-

dian lobe of the male adminiculum in these species, it is also supported as the sister species of *byersi* based on the large A9S lobe. A sister species relationship is also indicated between *madina* and *impudica* by the shared possession of tuberculate cuticle near the membranous lobe of the male eighth sternum, a feature not used in these analyses. Apparently, the spiny, transverse carina of the adminiculum found in the other species in this group has been lost in *impudica*, or at least is only present as an irregular edge.

Geographic distribution.—Colorado and Wyoming, westward to Oregon, Washington and southern British Columbia (Fig. 246). I could not locate Blakemore, Alberta in the Canada Geographic Name database, although "Blackmore Creek" British Columbia is near the Alberta border at the north end of Kinbasket Lake. The lack of specimens from western Wyoming and southern Idaho is probably due to a lack of collecting effort, as suitable habitats for *impudica* should occur there. A similar interruption in distribution is seen in several similarly distributed species, including *sackeni*.

Seasonal distribution.—April 5 to August 10. The collection dates (September 5–7) of the specimens from Palmer Lake, Colorado, are questionable as they fall a full month later than the next latest collection dates for *impudica* (August 1–10).

The seasonal range of *impudica* for a localized area probably extends for about a month, judging from collection records for Boulder (28 May to 27 June) and Chimney Gulch (5–29 June), Colorado. Earliest records are for April and May in the Pacific Northwest, with most Rocky Mountain records in June and July.

Habitat.—Virtually nothing is known of the habitats of this widespread species. At Uintah Canyon, Utah, I collected an adult of *impudica* in a pine and aspen woodland, with nearby open areas dominated by *Artemisia tridentata*.

Tipula impudica occurs at a wide variety of elevations, at approximately 230–900 m in the Pacific Northwest, and 1400–3000 m in the Rocky Mountains of Colorado, Wyoming and Utah.

Tipula (Eremotipula) madina Dietz

Tipula madina Dietz 1921: 6–7, fig. 3 (hypo., dor.), key; Alexander 1965b: 37, cat.; Theischinger & Theowald 1981: 28, cat.

Diagnosis.—Wings mostly unicolorous, without pale streak along vein A_1 and lacking yellowed c and sc cells (cf. *artemisiae*, *impudica*). **Male:** Hypopygium similar to others in *madina* group (outer basal lobe of ID broad and mostly smooth on lateral surface (Fig. 250) and crest of ID well-developed anteriorly, with wide groove between crest and upper beak), ventral lobes of A9S small and concealed, dorsolateral margin of BS without a spine (as in Fig. 205). **Female:** Low, pale inner ridge of the 8S (Fig. 243).

Description.—**Length:** Male 14–18 mm, female 19–24 mm long. **Head:** Vertex and postgena brownish gray, with orangish patches sublaterally on occiput. Antennal length: male 4–5 mm, female 3 mm. **Thorax:** Overall brownish gray (rarely yellowish brown), pruinose. Presutural scutum with two pairs of brown to dark brown, distinct lines. **Legs:** Femoral rings usually faint in males, distinct in females. **Wing:** Male 14–16 mm long, 4 mm wide; female 14–19 mm long, 3–4 mm wide. Overall light brown, stigma brown. Cells c and sc light yellow. Indistinct paler area around stigma and extending as band along cord into discal cell. Pale streak along middle section of vein A_1 in females only. **Abdomen:** Terga 2–6 often with dorsal and sublateral, light to dark brown patches, dorsal patches usually contiguous along abdomen, particularly in females; females with pale area between dark patches and lateral border of abdominal sclerites, giving appearance of dark and light lines. **Hypopygium:** *Ninth tergum:* Ratio of length $9T/BS = 0.5–0.6$. Dorsal lobes subparallel to slightly divergent (Fig. 247), each moderately long, slightly longer than basal width, narrowing to acute (Fig. 247) to subtruncate apex (Fig. 249), medial margin irregularly toothed. STP elongate, ratio of length $STP/9T = 0.5–0.7$, compressed, with dorsal ridge extending almost entire length, (nearly triangular in cross section), abruptly narrowed subapically, with apical fifth pale and dorsal margin weakly lacinate. Cuticle of STP not reticulate at 600 $\times$. Ventral lobes partially concealed beneath dorsal lobes, subparallel to slightly convergent (Fig. 248); each smooth, flat, with rounded to truncate apex; often a ventral ridge near apex. Ventral surface of shelf rugose, margin smooth. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of BS without projection opposite attachment of $sp1$. Dorsolateral margin of BS opposite posterior condyle of ID with slight, flat lobe with rounded margin. Ven-

tral lobes of A9S small and concealed, with dense, thickened, reddish brown, laterally directed setae. *Outer dististyle:* Posterodorsal margin straight, anterior extension of short to moderate length. *Inner dististyle:* Ventral surface of upper beak and apex of lower beak with well-developed ridges, lower beak truncate to rounded. Crest pale (Fig. 250), developed anteriorly along lateral surface of upper beak, with groove between crest and dorsum of beak equal to width of lower beak. Dorsal margin of crest usually shallowly concave, serrulate, nearly reaching OBL posteriorly; scattered spinules at base of crest. OBL large, $L/W = 1.4–1.9$, directed posteriorly and dorsal margin slightly bent laterally along posterior half, lateral surface smooth, flat, apex broad and rounded. *Adminiculum:* Lateral plates expanded, fused with dorsal lobes (Fig. 251), usually a well-developed, transverse carina with several teeth on upper surface of each lateral plate near base (Figs. 252, 253). Dorsal lobes completely separate between median lobe and dorsal spines, each lobe mostly flat, smooth, its inner edge upturned against median lobe, with 2–3 acute points dorsally, ending posteriorly in several minute teeth, a large spine along lateral margin. Median lobe large, about one-third height of total adminiculum and expanded posteriorly (Fig. 254), with lateral carina extending dorsally on either side from roughened ventral margin. A pair of indistinct to distinct, dorsoventral ridges below median lobe, each directed posteriorly. *Eighth sternum:* Yellow bands usually present. Posterior (sclerotized) margin biconcave. Membranous apical region with a band of long setae, 3–5 setae wide, band narrowly interrupted at midlength (not clearly visible externally), inner setae short, a thin sclerite with several setae at each end of row. Length of setae greater than half sternal length; setae with rounded carinae. Membranous lobe absent, area densely tuberculate. *Ovipositor:* 8T and 9T yellowish to darker brown, 9T sometimes partly shiny. 10T yellowish to reddish-brown, shiny, scarcely or not swollen posteriorly, sometimes slightly darkened posteriorly. Cerci elongate, slender, light reddish brown (often darker basally), only slightly upturned apically. 8S brown and pruinose basally, remainder pale and shiny, with reddish brown medially. Hypogynial valve blades with apices narrow to evenly rounded (Fig. 243). Each inner ridge of 8S low, pale (Fig. 243); pigmentation variable along

inner grooves, sometimes absent, outer pigmentation light brown.

Specimens examined.—*Type material*: Holotype ♂ (ANSP): UTAH: Utah Co., Provo, V-24-1912, T. Spalding, holotype #6393. The holotype lacks most of the right antenna and all legs except the tibia and tarsus of the right mesothoracic leg. Paratype: 1♂, topotypic. Hypopygium extensively dissected and broken, but conspecific with type.

Other specimens: 37♂, 4♀. USA: IDAHO: Gooding Co., 3 mi S Hagerman, 8-V-1968, R. Jones, on *Artemisia t. tridentata*, 1♀ (UIM). NEVADA: Lander Co., Kingston Camp, 30 mi S Austin, 2225m, 15-VIII-1966, F. P. & M. Rindge, 1♂, 1♀ (AMNH); White Pine Co., 9.8 km E of McGill, along Timber Creek, 2403 m, 14-VI-1986, JKG #399, 3♂ (ANSP, UK). UTAH: Juab Co., Eureka, (1949 m), 24-31-V-1920, 11-VI-1921, T. Spalding, 3♂ (ANSP); Piute Co., Tushar Mountains, City Creek Campground, 10 km NW Junction, 2320 m, 30-VI-1991, JKG #528, 1♂ (ANSP); Tooele Co., Little Valley Creek, Little Valley Campground, Sheeprock Mountains, (2134 m), 19-VI-1980, S. Vernon, R. W. & J. W. Bauermann, 2♂ (BYU); Johnson Pass, Stansbury Mountains, (2012 m), 11-VI-1955, at light, H. E. Cott, 1♂ (CAS); Utah Co., Provo, V-24-1912, (1387 m), T. Spalding, paratype of *Tipula spaldingi*, 1♂ (ANSP); Washington Co., 6.9 km E of Central, 1859 m, 29-IV-1986, JKG #365, 22♂ (ANSP, AMNH, CMNH, UK, UMAA); as preceding but pupa collected in soil under *Cowania mexicana*, male emerged 7-V-1986, 1♂ (JKG); Leeds Canyon, 16-VI-1978, W. Hanson, G. Knowlton, 1♂, 2♀ (USU); as preceding but also Oak Grove Camp, 5-VI-1964, at light, W. J. Hanson, 1♂ (USU); Mountain Meadows, (ca. 8 km N Central), 10-V-1936, B. E. Rees, B. Duncan, 1♂ (USNM); County unknown, Salt Lake, V-22, 1♂ (USNM).

Discussion.—Dietz (1921) considered the ninth tergum to be distinctive for *madina*, in that it is "... produced in the middle with a small central emargination". In fact, the structure of the ninth tergum is not as Dietz described. The dorsomedial lobes of the ninth tergum in the holotype are closely appressed (by compression of the entire hypopygium) with the apices not clearly visible, therefore appearing to Dietz as a single projection with an emarginate apex.

As noted for *impudica*, male specimens of *madina* show intraspecific variation involving the shape of the dorsal and ventral lobes of the ninth

tergum (Figs. 247, 248) and in the number of spines along the dorsal lobes of the adminiculum. Even though only a small number of specimens were examined, much of this variation in *madina* can be seen in specimens from a single series.

Males of *madina* are most likely to be confused with other members of the *madina* group (*byersi*, *impudica* and *spaldingi*) and *madina* can be distinguished from these three species using the characters listed in the key and diagnosis. In addition, the setal band of the eighth sternum is narrowly divided in *madina* and complete in the other three species; however, this is not an easily observed feature.

Female specimens are difficult to distinguish from other species of *Eremotipula*, particularly from *impudica*, *spaldingi* and *kaibabensis*. Since few specimens could be found clearly associated for the species I had difficulty assessing the variability in the wing patterns and inner 8S ridge. I have recognized females of *madina* by a mostly unstreaked wing, costal and subcostal cells not yellowed and a low, pale inner ridge of the 8S.

Relationships.—*Tipula madina* may be the sister species to *impudica* or *spaldingi* and these relationships are discussed further in the corresponding section for those species and the phylogenetic analyses. The spine on the basistylar margin, a probable synapomorphy for the *madina* group, is not seen in *madina* and is only present in certain parts of the range of its sister species, *impudica*.

Geographic distribution.—Western Utah to eastern Nevada, southern Idaho? (Fig. 246).

Seasonal distribution.—April 29 to August 15.

Habitat.—Information on habitats of *madina* is known for only two localities. At a site near Central, Utah, I collected numerous specimens, many teneral, among vegetation dominated by tree-sized *Cowania mexicana* (cliffrose), *Juniperus* trees, *Artemisia tridentata* and grasses. A male pupa was found in the soil under a *Cowania* shrub. Along Timber Creek, Nevada, I found this species in steppe vegetation of *Artemisia tridentata* and *Purshia tridentata*.

Tipula madina has been collected at elevations from 1300 m to 2400 m.

Tipula (Eremotipula) spaldingi Dietz

Tipula spaldingi Dietz 1921: 7-8, fig. 5 (hypo., dor.); Alexander 1965b: 38, cat.; Theischinger & Theowald 1981: cat.

T. spaldingi: Alexander 1948: 30, fig. 9, redesc. (misident. of *byersi* and *kaibabensis*).

Diagnosis.—Wing with cells r_5 , and m_1 – m_4 mostly pale, isolating brown patches in medial cells. *Male*: Hypopygium similar to others in *madina* group with outer basal lobe of ID broad, mostly smooth on lateral surface and crest of ID well-developed anteriorly, with wide groove between crest and upper beak, but distinguished by OBL with anterior protuberance and strongly narrowed apex (Fig. 258), dorsolateral margin of BS with short, curved spine (Fig. 257), median lobe of adminiculum greatly expanded laterally, deltoid in posterior aspect (Fig. 261). *Female*: Each inner ridge of 8S pale throughout, moderately high (Fig. 244).

Description.—*Length*: Male 17–20 mm, female 22–27 mm. *Head*: Vertex and postgena brownish gray, with orangish patches sublaterally on occiput. Antennal length: male 4–5 mm, female 3–4 mm. *Thorax*: Overall brownish gray, pruinose. Presutural scutum with two pairs of light to dark brown lines. *Legs*: Femoral rings indistinct in males, distinctly brown in females. Tibial apices with slight darkening. *Wing*: Male 15–19 mm long, 3–5 mm wide; female 16–19 mm long, 4–5 mm wide. Overall light brown; stigma brown. Cells *c* and *sc* faintly yellowed. Wing patterning exhibiting slight dimorphism: Males with pale area surrounding stigma, extending as band along cord through discal cell and into proximal sections of cells m_3 and m_4 ; pale streak along middle portion of A_1 (sometimes extending across to include cell *m*), streak sometimes in cell a_1 ; Females with outer half or more of r_5 pale, borders of cells m_1 – m_4 pale, often isolating brown areas within the cells, pale areas of a_1 often more extensive, isolating a triangular brown patch. *Abdomen*: Terga 2–6 usually with sublateral and dorsal brown patches, sometimes nearly contiguous along abdomen; females often with extreme lateral border of tergites pale, bordering brown patches. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.6. Dorsal lobes subparallel, each elongate, slightly longer than width at base (Fig. 255); medial margin minutely roughened, apex acute, slightly downturned. STP elongate, ratio of length STP/9T = 0.5–0.6, strongly compressed, with abruptly narrowed, pale apex and dorsal margin slightly lacinate. Cuticle of STP not reticulate. Ventral lobes partially concealed be-

neath dorsal lobes, slightly convergent (Fig. 256); each smooth, flat, with rounded to subtruncate apex, lobe sometimes with ventral ridge (as in *madina*). Ventral surface and margin of ventral plate smooth. *Ninth sternum* (+ *basistyle*): Dorso-medial margin of basistyle opposite attachment site of $sp1$ nearly straight. Dorsolateral margin opposite posterior condyle of ID with a short, thick, inwardly-curved apical spine (Fig. 257). Ventral lobe of A9S entirely membranous, with short, thickened, reddish brown setae restricted to dorsal edge; lobe partially concealed. *Outer dististyle*: Posterodorsal margin straight, anterior extension of moderate length. *Inner dististyle*: Ventral surface of upper beak with well-developed ridges, those of lower beak obsolete. Crest pale (Fig. 258), developed anteriorly along lateral surface of upper beak, with groove between crest and dorsum of upper beak usually equal to width of lower beak, sometimes narrower. Dorsal margin of crest usually straight or convex, rarely concave, serrulate, nearly reaching outer basal lobe posteriorly, scattered spinules at base of crest, tuberculate anteriorly. OBL large, L/W = 1.7–2.3, directed posteriorly and slightly bent laterally along posterior half, lateral surface mostly smooth, protuberance near anterior margin, sometimes extending posteriorly as ridge, apex strongly narrowed. *Adminiculum*: Lateral plates greatly expanded, narrowing slightly toward and fusing with dorsal lobes (Fig. 259); a transverse carina with numerous small teeth on upper surface of each lateral plate near base (Fig. 260). Dorsal lobes completely separate between median lobe and dorsal spine, each lobe with inner edge upturned against median lobe and laterally expanded perpendicular to median lobe, with several minute teeth dorsally along dorsal margin. Median lobe greatly expanded laterally with margins minutely serrulate, deltoid when viewed posteriorly (Fig. 261), beak distinct. *Eighth sternum*: Yellow bands indistinct. Posterior (sclerotized) margin biconcave. Membranous apical region with band of long setae, widest laterally and broadened at middle almost to membranous lobe. Setae over half as long as eighth sternum, with rounded carinae. Membranous lobe short (Fig. 262), rounded, about as long as wide, with single (ungrouped) microtrichia. *Ovipositor*: 8T yellowish brown, posterior margin slightly concave. 9T yellowish to reddish-brown, sometimes shiny. 10T yellowish to reddish-brown, shiny, more or less swollen posteriorly,

slightly darkened posterolaterally. Longitudinal apodeme only moderately developed, not strongly narrowed anteriorly. Cerci elongate, slightly to moderately upturned apically, yellowish to reddish brown. 8S light brown proximally, remainder yellowish brown, often darker brown or reddish brown medially. Hypogynial valve blades light reddish brown, apices narrowly rounded (Fig. 244). Each inner ridge of 8S well developed, pale; pigmentation scarcely reaching anteriorly to ridge, outer pigmentation sometimes absent (Fig. 244).

Specimens examined.—*Type material*: Holotype ♂ (ANSP): **UTAH**: Juab Co., Eureka, 1949 m, August 1, 1911, Tom Spalding. The specimen has no locality-date label, being merely labeled as Holotype #6392. Dietz (1921) published the data for the type. The type lacks most of both antennae and all but one leg; the head and right wing have been reattached.

None of the 9 paratypes is conspecific with the holotype; one paratype from Provo, Utah is *madina*, the others are *kaibabensis*.

Other specimens: 54♂, 30♀. **USA**: **IDAHO**: Butte Co., Craters of the Moon Natl. Monument, 14-VII-1965, at UV light, D. Horning, Jr., 1♀ (UIM); 6 mi S Howe, 1-VII-1981, at light, M. Stafford, 1♀ (UIM); Gooding Co., Tuttle, 13-VI-1959, R. B. Hawkes, 1♂ (UIM); Oneida Co., 5 mi NW of Holbrook, 8-VI-1972, Malaise trap, G. F. Knowlton, W. J. Hanson, 1♂, 2♀ (USU); Bear Lake Co., Giveout, 42°24'N, 111°10'W, 2042 m, 7-VII-1920, 1♂ (AMNH). **NEVADA**: Elko Co., Carlin, (1493 m), 26-VI-1953, A. B. Gurney, 1♂ (USNM); Elko, (1524 m), 19-V-1926, M. C. Van Duzee, 3♂, 1♀ (CAS); Moor Summit area, 14.5 km E of Wells on US Highway 80, 1859 m, 16-VI-1986, JKG #402, 2♂, 3♀ (ANSP); 13.0 km SW of Wells, Angel Creek Campground, 2134 m, 15-VI-1986, JKG #400, 1♂, 2♀ (ANSP); Wells, Angel Creek, 23-VI-1927, J. M. Aldrich, 2♂, 1♀ (USNM); Wells, (1715 m), 12-VII-1911, 20-23-VI-1927, J. M. Aldrich, 2♂, 1♀ (USNM); Lamoille Canyon, 4-VIII-1964, M. Gardner, 1♀ (UCD); Thomas Canyon Camp, 9 mi SSE Lamoille, 2286 m (7500 ft.), 5-VII-1966, F. P. and M. Rindge, 3♂, 1♀ (AMNH); Eureka Co., Emigrant Pass, 13-VI-1960, F. Parker, 2♀ (UCD); Eureka, 6900 ft (2103 m), 12-VI-1976, some collected from beaks of Brewer's Blackbirds (*Euphagus cyanocephalus*), GWB #1, CWY, 11♂, 7♀ (UK); as preceding but 27-VI-1921, T. Spalding, 2♀ (ANSP); Lander Co., Highway 21 at Highway 50,

5 mi ESE of Austin, 6750 ft (2057 m), 5-VIII-1964, H. B. Leech, 1♂ (CAS); White Pine Co., 9.8 km E of McGill, along Timber Creek, 2430 m, 14-VI-1986, JKG #399, 2♂ (UK); Wheeler Peak vicinity, 12.9 km W, 2.4 km N of Baker, 2682 m, 12-13-VI-1986, JKG #396, 5♂, 2♀ (ANSP, UK, UMAA); overlook on Wheeler Peak road, 12.9 km W, 0.8 km N Baker, 2804 m, 13-VI-1986, JKG #398, 1♀ (JKG). **OREGON**: Harney Co., Juniper Lake, VI-18-1951, B. Malkin, 1♂, 1♀ (USNM); P. Ranch, Donner und Blitzen (River) Valley, 22-VI-1922, E. Van Dyke, 1♀ (CAS); Malheur Co., Sucker Creek Canyon, 15-18-VI-1951, B. Malkin, 1♀ (USNM, exact mapped location undetermined). **UTAH**: Box Elder Co., Long Birch Creek, near headwaters, 16-VII-1980, Baumann and Clark, 3♂, 1♀ (BYU); 3.2 km SW of Rosette on Utah Highway 30, 1682 m, 16-VI-1986, JKG #403, 7♂, 3♀ (ANSP, AMNH, UK); Eureka Co., topotypic, 27-VI-1921, T. Spalding, 2♀ (ANSP); Juab Co., Trout Creek, Deep Creek Mountains, 27-VII-1982, Baumann and Cox, 6♂, 4♀ (ANSP, BYU); Tooele Co., Stockton, (1544 m), 30-V-1914, T. Spalding, 1♂ (MCZ); Utah Co., Payson Canyon, no date, V. Tanner, 1♀ (BYU).

Discussion.—Some confusion has surrounded the identity of *spaldingi*. Dietz's original description and diagrammatic illustration are not adequate to identify this species, particularly since the type series consists of three different species. Alexander apparently never examined the type of *spaldingi*. He based his redescription of it (Alexander 1948: 30) on two male specimens collected in Utah, one (with the genitalia slide-mounted) from Zion National Park and the other (with the body intact) from Bluff. I have examined both specimens; the one from Zion National Park is *byersi* and the Bluff specimen is *kaibabensis*. Alexander's redescription and illustrations of the hypopygium (Alexander 1948: Fig 7) clearly refer to *byersi*, in particular, his description of the ninth tergum, basistylar margin and dorsal lobes of the adminiculum ("gonapophyses"). The adminiculum has a shape unique to *byersi*.

Genitalic features such as the distinctive outer basal lobe, the spine on the basistylar margin, a short membranous lobe and the prominent expansion of the median lobe of the adminiculum are all clearly visible on the holotype male and conclusively establish the identity of *spaldingi*. No other specimens have been correctly assigned to this species prior to this study.

The spine on the basistylar margin varies slightly in development, with one specimen having only minute spines.

Although males of *Tipula spaldingi* are superficially similar to species such as *kaibabensis* or even *evalyinae*, based on the structure of the ninth tergum or inner dististyle, it is easily recognized as a member of the *madina* group on the basis of other male characters as noted in the key and diagnosis. In addition, the ventral lobe of the appendage of the ninth sternum is almost entirely membranous (mostly sclerotized in the other species) and the membranous lobe of the male eighth sternum is larger than in *impudica* and *byersi* (absent in *madina*).

Females can be recognized by the characters used in the key, particularly the streaked wing and high, pale inner ridge of the 8S.

Relationships.—The toothed margin of the dorsal lobes and thickened, carinate median lobe of the adminiculum provide evidence that *spaldingi* is closely related to *impudica* and *madina*, although little evidence supports a sister species relationship with either species.

Geographic distribution.—Northwestern Utah, northern Nevada and southern Idaho (Fig. 224).

Seasonal distribution.—May 19 to August 5. This species has been most often collected during middle to late June.

Habitat.—*Tipula spaldingi* has been collected in both open scrub and open woodland. George Byers and Chen Young collected this species at Eureka, Nevada, among shrubs comprised mostly of *Chrysothamnus*, where they observed heavy predation on the adults by Brewer's Blackbirds (*Euphagus cyanocephalus* Wagler) (Byers, field notes). I have collected *spaldingi* in *Artemisia-Purshia* steppe at the Timber Creek and Angel Creek sites in Nevada, and in *Juniperus* woodland with an undergrowth of *Artemisia*, *Chrysothamnus* and *Purshia* at Moor Summit, Nevada, and near Rosette, Utah. At some of the highest elevations known for the species, in the Wheeler Peak vicinity, adults were found on mostly open slopes with scattered *Pinus monophylla* and *Cercocarpus ledifolius*, and an undergrowth of stunted *Artemisia tridentata*.

Tipula spaldingi occurs at a wide variety of elevations, from 1500–2800 m.

The kaibabensis Species Group

This species group includes *anasazi*, *dimidiata*, *kaibabensis* and *mitrata*. Synapomorphies of the

four species are given in Fig. 22. *Tipula artemesia* is supported as the sister species to the *kaibabensis* group by weak characters.

Tipula (*Eremotipula*) *anasazi*, new species

Diagnosis.—Wing with pale streaks posteriorly, no contiguous pale spots as in *mitrata* (Fig. 447). *Male*: Hypopygium similar to others in *kaibabensis* group (outer basal lobe of ID small, concave laterally with a rounded apex, membranous lobe of 8S relatively long and slender); distinguished by long and slender setae on the ventral lobe of the A9S (Fig. 268), STP of medium-length and scarcely laciniate dorsally (Fig. 263), crest of ID emarginate dorsally (Fig. 266) and dorsal lobes of 9T short and strongly divergent (Fig. 263). *Female*: Each inner ridge of 8S well developed (unlike *mitrata*; Fig. 273), brown pigmentation laterally, but not dorsally along ridge (Fig. 278). Distributed in central New Mexico.

Description.—*Length*: Male 15–17 mm; female 18–21 mm. *Head*: Vertex and postgena dark brownish-gray, median line dark and distinct; a pair of reddish blotches sublaterally on occiput. Frontal tubercle usually slightly protuberant. Antennal length: male 4 mm long; female 2–3 mm. *Thorax*: Overall dark brown, pruinose; strongly contrasting orange- and cream-colored areas on all sclerites of pleura except katatergite and meron. Presutural scutum with strongly contrasting, dark brown stripes, remainder brown and pruinose (faint, medial stripe indicated on one individual). *Legs*: Femoral rings dark brown and distinct. *Wing*: Male 14–16 mm long, 3–4 mm wide; female 15–17 mm, 4 mm. Overall light brown; stigma brown. Pale area surrounding stigma and extending as band along cord and into cells r_{4+5} , m_1 , m_2 and discal cell; pale streaks also along veins Cu, CuA₂, A₁ and in cell a_1 (Fig. 447). (Wings of specimens from Sandoval Co. darker overall than those of specimens from Bernalillo Co.). *Abdomen*: Overall mottled brown and yellowish brown, shiny; tergum 1 with some pruinosity. Terga 2–6 each with dorsal and lateral thick, dark brown patches in specimens from Sandoval Co.; only lateral patches distinct in specimens from Bernalillo Co. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.7. Dorsal lobes divergent, each moderately extended, slightly wider at base than long (Fig. 263); medial margin irregular, angulate near midlength, lateral mar-

gins smooth, apex acute. STP elongate, ratio of length STP/9T = 0.5–0.6, scarcely compressed (dorsally rounded); narrowed and pale apically, dorsal margin serrulate to slightly laciniate. Cuticle reticulate at base of STP, becoming plicate distally. Edge of 9T with short spine often at upper corner, sometimes blunt. Ventral lobes concealed beneath dorsal lobes, slightly convergent (Fig. 264), smooth, with rounded apices slightly curved dorsad. Cuticle of ventral plate reticulate to striate, margin smooth. *Ninth sternum* (+ *basistyle*): Dorsolateral margin of basistyle slightly produced opposite condyles of inner dististyle. Ventral lobe of A9S without pronounced basal swelling, proximally with few setae, 1–2 scarcely thickened and pale (Fig. 268). *Outer dististyle*: With straight to slightly convex posterodorsal margin, anterior extension short to moderate. *Inner dististyle*: Ventral surface of upper beak with strong ridges, lower beak smooth. Crest pale (Fig. 266), arising along dorsal margin of upper beak, with slight gap anteriorly between crest and beak, margin serrate anteriorly, microscopically serrulate posteriorly, emarginate dorsomedially, crest rounded posteriorly. OBL small, lateral surface slightly concave, directed posteriorly, L/W = 1.2–1.7, with indistinct ridges parallel to ventral edge, apex wide and rounded. *Adminiculum*: Two thin, elongate arms arising anteriorly from adminiculum and directed dorsally (Fig. 270), apices subacute and slightly curved. Dorsal lobes of lateral plates slightly separated, each lobe pale, upturned, with rounded, smooth apex (Fig. 269). Median lobe large, pale, rounded, without beak, with a large, dorsoventral ridge along each side. *Eighth sternum*: Two yellowish, longitudinal bands from base to apex. Posterior (sclerotized) margin shallowly concave. Membranous apex with an irregular, sparse (2–3 setae wide) band of long setae, widest laterally, setae microscopically carinate. A pale, flat, membranous lobe immediately posterior to long setae (Fig. 265), lobe about 2x as long as width at base (Fig. 267), with dense, singly spaced, long microtrichia. *Ovipositor*: Each inner ridge of 8S well developed, broadly and abruptly expanded at base of hypogynial valves (Fig. 273); brown pigmentation extending along basal outer surface, pale along top of ridge; inner surface pale (Fig. 278).

Specimens examined.—*Type material*: Holotype ♂ (UK): NEW MEXICO: Bernalillo Co., Sunset Cyn., T10N, R4E, 1, Albuquerque, larvae coll. IV-9-1983, in soil under shrubs, J. Gelhaus #207. The

holotype bears an additional label reading: "J. Gelhaus Rearing #207/pupa IV-20/m emerg. since V-4/in copula f#14/larvae, pupae in ETOH m #12". Paratypes: NEW MEXICO: Bernalillo Co., topotypes, Sandia Mountains, emerged IV-30 to V-8-1983 [9♂, 5♀; 10 specimens in ETOH with associated larval and pupal exuviae] (ANSP, UK, USNM); topotypes, 23-V-1979, 5400 ft [I record this as 1920 m], GWB #1 and party, JKG #79-20, 79-22, 18♂, 15♀ (ANSP, BYU, UK, UMAA, USNM); Sandoval Co., 6.6 km S Jemez Springs on NM Hwy. #4, 1798 m, at light, V-3-1986, JKG #373, 5♂ (ANSP, CMNH, UK).

Etymology.—*Tipula anasazi* is named for the early Native American people, the Anasazi, who occupied the general region where this crane fly species now occurs.

Discussion.—*Tipula anasazi* can be distinguished from the other members of the *kaibabensis* group and *artemisiae* by the characters listed in the key and diagnosis. In addition, the posterolateral corner of the ninth tergum of *anasazi* is often produced into a short spine, and the range of this species is not known to overlap those of the other four species.

Relationships.—The elongate, dorsally-directed processes of the adminiculum, a feature found within *Eremotipula* only in males of *Tipula anasazi* and *T. mitrata*, indicates a close relationship between these two species. Other similarities in male characters, possibly synapomorphies, include the shape of the ventral lobes of the ninth tergum, the short and slightly concave outer basal lobe of the inner dististyle and the flat, membranous lobe of the eighth sternum.

Geographic distribution.—Central New Mexico (Fig. 279).

Seasonal distribution.—All flight records for this species are in May.

Habitat.—Both sites in which *Tipula anasazi* have been found (canyons in the Sandia and Jemez Mountains) have vegetation typical of Great Basin conifer woodland (Brown 1982a), including dominants of *Juniperus* sp. and *Cercocarpus* sp. with understory shrubs of *Cowania mexicana*, *Chrysothamnus* sp., *Atriplex* sp., and also *Opuntia* spp. and various grasses and herbaceous annuals. Adults were abundant in the shrubs at Sunset Canyon in late May 1979, and larvae were collected in April 1983, but no adults or immatures were found at similar times in 1981 and 1986, the latter two years classified as drought years of insufficient precipitation during the fall and winter.

Mature larvae collected in early April occurred in the top 2.5 cm of soil under a thin litter of stems and leaves, under or surrounding shrubs of *Chrysothamnus* sp. and *Cowania mexicana*.

Tipula (*Eremotipula*) *mitrata* Dietz

Tipula mitrata Dietz 1921: 11–12, fig. 10 (male 9S; ID, dor.), key; Alexander 1946a: 508; Alexander 1965b: 37, cat.; Theischinger & Theowald 1981: 30, cat.

Diagnosis.—Wing with three contiguous pale areas in cell *m* and along vein A_1 (Fig. 454). **Male:** Hypopygium similar to others of *kaibabensis* group (outer basal lobe of ID small, concave laterally with rounded apex; membranous lobe of 8S long and narrow), ventral lobes of A9S with one or two greatly thickened, black spiniform setae (Fig. 282); membranous lobe between eighth and ninth sterna flat and bare, lobe nearly equal in length to setae in band (Fig. 286). **Female:** Each inner ridge of 8S moderately developed (not as developed as others in *kaibabensis* group), brown pigmentation laterally, but pale along ridge dorsally (Figs. 275, 276).

Description.—**Length:** Male 15–17 mm (specimens in alcohol 18.5 mm), female 17–24 mm. **Head:** Vertex and postgena brownish gray, with irregular orange blotches sublaterally on occiput. Antennal length: male 4–5 mm, female 2–3 mm. **Thorax:** Overall brown, pruinose. Presutural scutum with two pairs of distinct, brown stripes; median area between inner stripes light brown or bright yellowish brown, remainder light brown and pruinose. **Legs:** Femoral ring brown and distinct. **Wing:** Male 14–16 mm long, 3–4 mm wide; female 13–19 mm long, 3–5 mm wide. Overall light brown, stigma and cell *sc* yellowish brown. Pale area surrounding stigma and extending as band along cord to proximal half of discal cell, also along *Cu*, and A_1 ; in female, nearly always with pale area in front and behind vein A_1 (at two thirds length); pale area generally extending into bordering section of cell *m* (Fig. 454). **Abdomen:** Terga 1–8 light brown to more usual bright yellowish-brown, shiny. Terga 2–6 each with a sublateral brown patch, nearly contiguous in most, dorsal spots in females, usually reduced. **Hypopygium:** **Ninth tergum:** Ratio of length 9T/BS = 0.5. Dorsal lobes slightly divergent (Fig. 280), each moderately long, about as long as wide, apical margin irregular to toothed. STP elongate, ra-

tio of length STP/9T = 0.5–0.6, somewhat compressed, dorsal ridge distinct in holotype, indistinct in others, pale near apex, dorsal margin serrulate subapically. Cuticle faintly reticulate at base of STP. Ventral surface of shelf reticulate, with smooth margin. Ventral lobes visible from above, subparallel (Fig. 281); each lobe smooth, flat, with rounded apex slightly curved dorsad. **Ninth sternum (+ basistyle):** Dorsolateral margin of BS only slightly produced opposite posterior condyle of ID. Ventral lobes of A9S small, with apical portion directed posteriorly, not ventrally, base of appendage with usually 1, sometimes 2, thick, dark, slightly curved spiniform setae (Fig. 282); a few setae elsewhere on ventral lobe, one or more slightly thickened. **Outer dististyle:** With straight posterodorsal margin, anterior extension long. **Inner dististyle:** Ventral surface of upper beak with strong ridges, few weak ridges on apex of lower beak. Crest pale (Fig. 283), posterior lobe moderate-sized and rounded, nearly reaching OBL, margin microscopically serrulate. OBL short, with scarcely any free lobe portion, lateral surface concave, directed posteriorly, L/W = 1.2–1.5, ridge parallel to ventral edge, apex wide and rounded. **Adminiculum:** Two elongate, slightly twisted arms arising anteriorly from adminiculum and directed dorsally (Figs. 284, 285). Dorsal lobes of lateral plates slightly separated, each lobe narrow and smooth. Median lobe relatively large, height about one third total height of adminiculum, lobe with short beak; a distinct dorsoventral ridge near base along each side. **Eighth sternum:** Posterior (sclerotized) margin shallowly concave. Membranous apex with irregular, sparse (2–4 setae wide) band of setae, widest medially; a small sclerite with setae at either end. Setae microscopically carinate, beset with small points (Fig. 287). A pale, flat membranous lobe immediately posterior to long setae (Fig. 286), lobe about 4x as long as width at base; lobe and membrane surrounding its base glabrous and rugulose. **Ovipositor:** Inner ridge of 8S moderately developed, expanded at base of hypogynial valves; brown pigmentation extending along basal outer surface, pale along top of ridge (Figs. 275–276; inner surface pale posteriorly, pigmentation only at base. Vaginal apodeme dark, elongate, slender.

Specimens examined.—**Type material:** Holotype ♂ (ANSP): NEW MEXICO: Grant Co: Silver City, 25-V-1913, Holotype #6396. The holotype is

in fair condition, lacking all flagellomeres of antennae and the left wing, and with one leg and two leg parts remaining. Although Dietz recorded the date of collection as "May 26", I interpret the number on the collection label as "25."

Other specimens: ARIZONA: Cochise Co., Chiricahua Mountains, Rucker Forest Campground, 1981 m, 24-V-1993, at light, JKG #596, C. Nelson, D. Koenig, 1♀ (ANSP); Dragoon Mountains, Cochise Stronghold Campground, 14.5 km W Pearce, 1525 m, 25-V-1993, at light, JKG #597, C. Nelson, D. Koenig, 5♂, 5♀ (ANSP); Gila Co., Pinal Creek, Pioneer Pass Recreation Area, Pinal Mts. [12 km S Globe, 1829 m], 5-VI-1982, Baumann and Clark, 1♂, 3♀ (BYU, UK); Gila-Pinal Cos., Miami, Pinal Mts., 5000 ft [1524 m], 11–25 May 1925, at light, O. C. Poling (det. as *coconino* by J. S. Rogers, 2 specimens completely slide mounted), 12♂, 10♀ (ANSP, UMAA, UK, USNM); Graham Co., Pinaleno Mountains, Stockton Pass Picnic Ground, 11.3 km W Bonita, 1676 m, 11-IV-1986, at light, JKG #329, 1♀ (ANSP) as preceding but 26-V-1993, at light, JKG #598, C. Nelson, D. Koenig, 4♂, 5♀ (ANSP); Greenlee Co., White Mountains, Granville Campground, 16 km NW Clifton, 2100m, 28-V-1993, at light, JKG #600, C. Nelson, D. Koenig, 3♂ (ANSP); Pima Co., Baboquivari Canyon, 9-IV-1963, Timberlake Coll., 3♀ (UCR); Browns Canyon, Baboquivari Mountains, 8-VI and 5-VIII, 1952, Cazier, Gertsch, Schrammel, 2♀ (AMNH); Santa Rita Mountains, Box Canyon, 19.3 km SE Continental, 4-VI-1991, ca. 1500m, ex. shaded rock crevice along arroyo, JKG #521, C. R. Nelson, 1♀ (ANSP); Santa Cruz Co., Kane Ranch, 17-IV-1950, R. Miller et al., 2♀ (UMAA); Pena Blanca, 20-IV-1969, W. Hanson, 1♀ (USU); Yavapai Co., Oak Creek Canyon, 25-V-1950, R. Miller et al., 3♀ (UMAA); County ?, Grand Canyon National Monument (Park), 25-IV-1958, rock holes on (along?) water, L. Nielson, 4♀ (USNM). NEW MEXICO: Grant Co., topotypic, 3-VI-1913, 1♀ (ANSP); Lincoln Co., Jicarilla Mountains, near Jicarilla, 27-V-1991, at light, JKG #508, C. Nelson, 23♂, 10♀ (ANSP).

Discussion.—Although one of the most readily identifiable species of *Eremotipula* due to the unique, black spiniform setae of the A9S in the males, *Tipula mitrata* remained unknown for over 65 years, in part, because Dietz neglected to mention these setae in the original description. In the holotype, the appendages of the ninth sternum are partially concealed, but the setae are still visi-

ble. Dietz does mention the small outer basal lobe and the elongate, membranous lobe between the eighth and ninth sterna, both features of importance in distinguishing this species from many others in the subgenus. Dietz cautioned that the membranous lobe in *mitrata* "must not be confounded with the median process (= membranous lobe) as found in *pellucida* . . ." in that the lobes in the two species arise in different areas of the eighth sternum and the lobe in *pellucida* is sclerotized. In fact, the membranous lobes in the two species are clearly homologous and both arise between the eighth and ninth sterna above the ventral point of the antecosta of the 9S.

The easily observable, spiniform setae of the appendages of the ninth sternum serve to separate males of *mitrata* from any other species of *Eremotipula*. Females can be recognized by the wing and genitalic characters listed in the key. In addition to those features, the abdomen is generally bright yellowish brown, polished, with distinct, dark brown lateral markings.

Relationships.—Both *mitrata* and *anasazi* possess elongate dorsal arms of the male adminiculum, a unique, unreversed synapomorphy, and provides strong support for a sister species relationship.

Geographic distribution.—Central Arizona to southwest New Mexico (Fig. 279).

Seasonal distribution.—Flight records are from early April to early August.

Habitat.—*Tipula mitrata* has been collected at a variety of habitats, at elevations from 1500–2100 m. The Lincoln Co., New Mexico site has habitat dominated by ponderosa pine (*Pinus ponderosa*), pinyon pine (*Pinus* sp.), alligator juniper (*Juniperus deppeana*), with an understory of scrubby oaks (*Quercus* sp.). The sites in the Dragoon and Pinaleno Mountains, AZ have woodland of *Juniperus deppeana* and live oak (*Quercus* sp.), with shrubs of manzanita (*Arctostaphylos* spp.), and *Rhus* sp., mountain mahogany (*Cercocarpus* sp.) and madrone (*Arbutus* sp.). The Box Canyon, Arizona site was open woodland of live oak, juniper and mesquite (*Prosopis* sp.), with *Yucca*, *Dasyllirion* and grasses (Gelhaus, field notes). Judging from the elevations at which many of the central Arizona specimens were collected (1524–1829 m), *T. mitrata* occurs within the transition zone of interior chaparral and Madrean evergreen woodland (Brown 1982b, Pace & Brown 1982b).

Tipula (*Eremotipula*) *dimidiata* Dietz

Tipula dimidiata Dietz 1921: 12–13, fig. 8 (male 9T), key; Alexander 1946a: 506; Alexander 1965b: 35, cat.; Theischinger & Theowald 1981: 16, cat.

Tipula (*Lunatipula*) *coconino* Alexander 1946a: 504–505, fig. 6, (male 9T, ID, OD); Alexander 1965b: 35, cat.; Theischinger & Theowald 1981: 14, cat.; Teale 1984: 30, misident. of *Tipula kaibabensis*. **NEW SYNONYMY.**

Diagnosis.—Wing without extensive pale blotches in cells *m* and *a*₁ (Figs. 448–449). **Male:** hypopygium similar to others in *kaibabensis* group (outer basal lobe of ID relatively small, excavated laterally with a rounded apex); ventral lobe of A9S with thickened yellowish setae (Fig. 291), outer basal lobe of ID with few weak ridges ventrally (Fig. 292); membranous lobe of 8S short and concealed, with long setae arising from apex (Fig. 295). **Female:** As in *nitrat*a (in dried specimens each inner ridge of 8S not appearing erect and well developed) (Figs. 272, 277).

Description.—**Length:** Male 15–17 mm (holotype of *dimidiata*: 10.7 mm), female 18–22 mm. **Head:** Vertex and postgena brownish gray, usually with orange patches sublaterally on occiput. Antennal length: male 4–5 mm, female 2–3 mm. **Thorax:** Overall brown, pruinose. Presutural scutum with two pairs of brown to dark brown stripes, median area between inner stripes yellowish brown to brownish gray, and pruinose, remainder of sclerite light gray. **Legs:** Femoral rings brown and distinct. Tibiae with slight apical darkening. **Wing:** Male 14–17 mm long, 3–4 mm wide (holotype of *dimidiata*: 10.9 mm long, 2.6 mm wide); female 16–17 mm long, 4 mm wide. Overall light brown; stigma brown. Cell *sc* yellowed. Pale area distal to stigma and extending as band along cord, more contrasting in females. Pale streak along vein A₁ and near vein A₂, isolating a light brown triangular area in cell *a*₁; most conspicuous in females, scarcely discernible in males. **Abdomen:** Terga 2–6 each with sublateral, dark brown patches, patches nearly continuous along abdomen in some individuals; a similar dorsal line usually absent. Abdomen overall bright yellowish brown. **Hypopygium:** **Ninth tergum:** Ratio of length 9T/BS = 0.5–0.6. Anterior border distinctly sclerotized along entire length, acrotergite complete dorsally, only slightly thickened laterally. Dorsal lobes subparallel to slightly divergent, each elongate, longer than width at base (Fig. 288); margin

irregular, apex usually acute and curved ventrad. A ventromedial flange extends from near apex of each lobe to base of STP. STP elongate, ratio of length STP/9T = 0.8–1.0, dorsal ridge well developed and extending nearly entire length, abruptly narrowing to acute apex; apex usually directed slightly ventrally. Dorsal margin smooth basally, pale and finely serrulate near apex. Cuticle of STP reticulate near base, becoming plicate apically. Ventral lobes partially visible from above, slightly convergent (Fig. 289), each lobe flat, smooth, with rounded to subacute apex. Cuticle of ventral shelf rugose, anterior margin plicate. **Ninth sternum** (+ *basistyle*): Dorsomedial margin of BS with acute extension projecting ventrally toward sp1 (as in Fig. 302), extension sometimes with one or two dark setae. Dorsolateral margin of basistyle only slightly produced opposite posterior condyle of ID. Ventral lobes of A9S small, with dense, thickened, short, reddish brown setae (Fig. 291), directed laterally. **Outer dististyle:** With straight posterodorsal margin, short anterior extension. **Inner dististyle:** Ventral surface of upper beak with few ridges, apex of lower beak with many ridges; in some individuals, ridges of lower beak well developed, markedly so in specimen from Double Springs. Crest pale (Fig. 292), with slight gap anteriorly between crest and beak, upper margin slightly convex and microscopically serrulate, with large rounded lobe posteriorly. OBL short, lateral surface concave, of nearly uniform width throughout and directed posteriorly, L/W = 1.7–2.1, irregular ridges near ventral edge (few in holotype of *coconino*), apex rounded, not narrowed. **Adminiculum:** Each lateral plate expanded basally, narrowing to apex (Fig. 293), excavated posteriorly; small process on either side of dorsal spine (Fig. 294). Dorsal lobes of lateral plates rounded apically, slightly separated; each with several striae. Median lobe large, height about one third total height of adminiculum, without beak; slight ventral carina. **Eighth sternum:** Two faint, yellowish, longitudinal bands from base to apex, on either side of basal notch. Posterior (sclerotized) margin shallowly concave. Membranous apex with irregular band of sparse setae, about two setae wide, setae over half to nearly equal to sternal length; thin sclerite with several setae at either end of setal row. Setae microscopically carinate. A knob-shaped, pale membranous lobe (Fig. 296), slightly wider than long, concealed between eighth and ninth sterna, lobe with patch of long

setae on posterior surface near apex (Fig. 295), glabrous anteriorly. *Ovipositor*: Each inner ridge of 8S moderately developed (in dried specimens, ridges not erect as in *kaibabensis* but lay horizontal along median), broadly expanded at base of hypogynial valves; light brown pigmentation extending along basal outer surface, pale along top of ridge; inner surface pale anteriorly, pigmentation only basally (Figs. 272, 277). Vaginal apodeme dark, elongate, slender.

Specimens examined.—*Type material*: *Tipula dimidiata* Dietz. Holotype ♂ (ANSP): NEW MEXICO: Grant Co, Silver City, 1-VI-1911, Holotype #6399. Specimen in good condition but lacking all legs except right front, and lacking terminal flagellomeres of antennae.

Tipula coconino Alexander. Holotype ♂ (USNM): ARIZONA: Coconino Co., Williams, 11-VI-1941, J. Sperry. Hypopygium of holotype mounted on microscope slide. Allotype ♀: on same pin as holotype. Paratype, 1 ♂, topotypic.

Other specimens: USA: ARIZONA: Coconino Co., Kaibab Lake, 4.8 km NE Williams, 2073 m, emerged V-21–23–1986 in lab., JKG #369, 2 ♂, 2 ♀ (ANSP); same but coll. 9-VI-1979, GWB #2, 31 ♂, 1 ♀ (CAS, CMNH, UK); Williams, V-25 to 4-VI, no year, H.S. Barber, 5 ♂, 1 ♀ (with assoc. pupal skin) (ANSP, USNM); Oak Creek, 5-VI-1949, N. Cricknar, 2 ♂ (ANSP, NMNH); Oak Creek Canyon, Bootlegger camp area, 11-VI-1979, 5300 ft (1615 m), GWB #3, 1 ♂ (UK); Double Springs camp, W side of Lake Mormon, 11-VI-1979, 7140 ft (2134 m), GWB #5, 1 ♂ (UK). Mohave Co., Hualapai Mountain Park, 15 km ESE Kingman, 1460m, 26-V-1979, GWB #2, JKG, 2 ♀ (UK); same as preceding but Pine Knoll campground, 8-VI-1982, Baumann and Clark, 1 ♂ (BYU); same but Wheeler Spring, 1 ♂ (BYU). Yavapai Co., Yarnell, Weaver Mts., V-23–29–1937, L.K. Gloyd, 1 ♂, 1 ♀ (UMAA). NEW MEXICO: Grant Co., topotypic, 26-V-1913, 1 ♀ (ANSP). UTAH: Washington Co., Snow Canyon, Dixie State Park (now Snow Canyon State Park), 15-IV-1962, G. Knowlton, 2 ♂ (USNM); St. George, 14-IV-1962, G. Knowlton, 1 ♂ (USNM).

Discussion.—Some variation is seen in the shape of the dorsal lobes of the ninth tergum of the male. In the holotype male of *coconino*, each lobe is broad with a subacute apex (as in Fig. 288); in the specimen from Double Springs, each lobe has a truncate apex (Fig. 290).

The holotype of *dimidiata* is an exceptionally small specimen but otherwise agrees in all fea-

tures with the other specimens examined including the holotype of *coconino*. Dietz (1921 fig. 8) illustrated the dorsal and ventral lobes of the 9T; he shows the dorsal lobes ("canthi") as short and acute, and the ventral lobes as exposed and acute ("lateral margin ends in an acute spine"). I examined the holotype and found that the dorsal lobes are much longer than drawn by Dietz, and have acute, slightly down-turned apices. The ventral lobes are flat with slightly rounded apices in the holotype, and, in addition, are mostly concealed in dorsal aspect. Dietz made no mention of the adminiculum.

Certain aspects of the original description and figures of *Tipula coconino* (Alexander 1946) are also misleading or inaccurate. Alexander states that the wing is "more heavily infuscated in outer radial field and as a broad seam along m-cu"; the wings appeared unicolorous in these areas when I examined the type specimens. The ventral lobes of the 9T are not "blackened blades" but instead are reddish brown, similar to the surrounding sclerotized cuticle. His figure of the inner dististyle shows the mesal surface of this structure, although the figure of the outer dististyle is of the lateral surface. The "microscopic teeth" of the lower beak of the ID are in fact the lateral aspect of the ridges of the beak. Alexander omits any mention of the adminiculum and eighth sternum. The sterna are severely torn and distorted on the holotype and paratype slides, with the membranous lobe crumpled and most of the apical setae broken off. The holotype slide of *coconino* does provide a good lateral view of the adminiculum.

Males of *Tipula dimidiata* can be confused only with those of *kaibabensis*, *anasazi* and *mitrata* (all species in the *kaibabensis* species group) but can be distinguished by the characters in the key and diagnosis. *Tipula dimidiata* and *kaibabensis* are particularly similar in genitalic structure of the male. Other important differences between *dimidiata* and *kaibabensis* in addition to those listed elsewhere are as follows: In *dimidiata*, the anterior extension of the outer dististyle is short, the margin of the subtergal process is finely serrulate, and the dorsal lobes of the adminiculum have several striae; in *kaibabensis*, the outer dististyle has a long anterior extension, the margin of the subtergal process is often lacinate, and the dorsal lobes of the adminiculum lack striae.

The female ovipositor of the one specimen cleared and examined appears very similar to that

of *mitrata* including the dark slender vaginal apodeme. The wing pattern can be used to distinguish between the two species, as the wing of *mitrata* shows more extensive pale areas in cells *m* and *a*₁ (Fig. 454), other than the typical streaking found in *dimidiata* (Fig. 448).

Relationships.—Several characters found in the male genitalia of *Tipula dimidiata* and *kaibabensis* support the hypothesis that these two taxa are sister species (see phylogenetic analyses).

Geographic distribution.—Southwest Utah, west-central Arizona to southwestern New Mexico (Fig. 297).

Seasonal distribution.—All flight records for this species are from mid-April to mid-June.

Habitat.—Along the Mogollon Rim, *Tipula dimidiata* inhabits ponderosa pine (*Pinus ponderosa*) woodland at elevations ranging from 1600 to 2100 m. No specific habitat data is available with the collections from western Arizona (Hualapai and Weaver Mts.), although ponderosa pine forest does occur in the Hualapai Mountains and it is likely that this is where the specimens were collected. Understory vegetation in these forests is generally sparse, ranging from *Chrysothamnus* sp. (more common in open areas of forest) and grasses at Kaibab Lake to deciduous oaks (*Quercus* sp.) and grasses at Double Springs (Gelhaus, field notes).

Adults, including some teneral individuals, were collected late in the day (7:15PM to 8:00PM) on sunlit areas of *Chrysothamnus* shrubs at the Kaibab Lake site in 1979. Pupal skins were common under these shrubs, occurring in or on the litter (GWB, JKG, field notes). In early May of 1986, I made a search for larvae of *Tipula dimidiata* at the same site and found the species to be rare. Only five larvae were found after a search of the soil under approximately 45 shrubs of *Chrysothamnus*; each larva was found under a separate shrub. Larvae were in loose to compacted soil under a 2.5 cm layer of *Chrysothamnus* and grass detritus.

Tipula (*Eremotipula*) *kaibabensis* Alexander

Tipula kaibabensis Alexander 1946a: 506–508, fig. 7 (male 9T, OD, ID, 9S, 8S); Alexander 1965b: 36, cat.; Theischinger & Theowald 1981: 24, cat.

Tipula coconino: Teale 1984: 30, redesc., key, loc.

Diagnosis.—Wings with pale streaks along vein A₁, usually broadly expanded into apical

portion of cell *m* and at base of cell *a*₁ (Figs. 450–453). *Male*: Hypopygium as in *kaibabensis* group (outer basal lobe of ID small, excavated laterally with rounded apex; membranous lobe of 8S elongate, slender), reddish-brown, thickened setae on the ventral lobe of A9S, OBL with strong ridge ventrally (Fig. 303); membranous lobe of 8S (Fig. 306) with microtrichia. *Female*: Each inner ridge of 8S well developed, abruptly and broadly expanded at base of hypogynial valves, usually darkened (Fig. 274).

Description.—*Length*: Male 15–18 mm, female 15–24 mm. *Head*: Vertex and postgena yellowish to brownish gray, usually with irregular orange patches sublaterally on occiput. Antennal length: male 4–6 mm, female 2–3 mm. *Thorax*: Overall brown to yellowish brown, pruinose. Presutural scutum with two pairs of distinct, dark brown to light brown stripes; median area between inner stripes yellowish brown to brownish gray, remainder of scutum pruinose. *Legs*: Femoral ring brown and distinct; tibia with slight darkening at apex. *Wing*: Male 14–17 mm long, 3–4 mm wide, female 12–19 mm long, 3–4 mm. Overall light brown; stigma slightly darker. Pale area surrounding stigma and extending as band along cord to cell *m*₄, a pale streak rarely along A₁ in males (Fig. 450); females with pale streaks along vein A₁, broadly expanded into apical portion of cell *m* and at base of cell *a*₁ (Figs. 451–452). *Abdomen*: Terga 2–6 each with sublateral brown to dark brown patches, sometimes nearly contiguous along abdomen; terga occasionally with light brown to brown, dorsomedial line, darkest anteriorly. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.6. Dorsal lobes slightly divergent, each elongate, slightly longer than width at base; apex acute to truncate, when acute, apices curved ventrally and slightly convergent, dorsal margin slightly irregular. Ventromedial flange extending from near apex of each lobe to base of STP. STP elongate, ratio of length STP/9T = 0.7–0.9, somewhat compressed, abruptly so near apex, with dorsal ridge extending from base to midlength, pale subapically; dorsal margin serrulate to weakly lacinate. Cuticle of STP near base without reticulations, plicate beyond base. Ventral lobes partially visible from above, slightly convergent (Fig. 298), each lobe small, parallel-sided, usually with rounded apex. Cuticle of ventral shelf reticulate, anterior margin entire. *Ninth sternum* (+ *basistyle*): Dorsomedial margin with acute extension

projecting ventrally to sp1 (Fig. 302). Dorsolateral margin of BS only slightly produced opposite posterior condyle of ID. Ventral lobe of A9S with dense, thickened, short, reddish brown setae, directed laterally. *Outer dististyle*: Posterodorsal margin straight, long anterior extension. *Inner dististyle*: Ventral surface of upper beak and apex of lower beak with strong ridges. Crest pale (Fig. 303), upper margin straight and microscopically serrulate, a rounded lobe posteriorly. OBL short, L/W = 1.7–2.4, lateral surface deeply concave and directed posteriorly, its ventral edge usually continuing as ridge (most visible in dried specimens), surface otherwise with wrinkles, apex rounded, not strongly narrowed. *Adminiculum*: Each lateral plate expanded basally, narrowing to apex, excavated posteriorly (Fig. 304); small roughened dorsal process on either side of dorsal spine (Fig. 305). Dorsal lobes of lateral plates separated, narrow, apex rounded with ridge. Median lobe large, slightly expanded ventrally with indistinct beak; slight dorsoventral carina present. *Eighth sternum*: Yellow longitudinal bands indistinct or absent. Posterior (sclerotized) margin shallowly concave. Membranous apex with irregular, thin band of setae, about three setae wide, band increasing in width laterally, usually narrowly divided at midlength, sometimes complete; thin sclerite with several setae at either end of setal row. A medial, elongate membranous lobe (Fig. 306), lobe over 3.5–6.0x as long as width at base, apex usually curled slightly; rugose at base, remainder with singly placed microtrichia. *Ovipositor*: Each inner ridge of 8S well developed, abruptly and broadly expanded at base of hypogynial valves (Fig. 274); brown pigmentation usually extending over entire outer surface including top of ridge; inner surface extensively darkened, often entire length of ridge. Vaginal apodeme diamond shaped anteriorly, brown, of moderate length.

Specimens examined.—*Type material*: Holotype ♂ (USNM): ARIZONA: Coconino Co., Grand Canyon, Kaibab Plateau, 8000 ft, 18-VI-1942, CPA. Condition good except missing all legs on right side, body intact, hypopygium not mounted on microscope slide. Paratypes: 3♂, topotypic, 17–18 June 1942 (USNM).

Other specimens: : ARIZONA: Coconino Co., topotypic, 2♂, 1♀ (USNM), (although topotypic, these specimens were not included in the type series by Alexander); Grand Canyon, 1929, 2♀ (USNM); 11 km E Jacob Lake, 2073 m (6800 ft), 21-VII-1965,

F. P. & M. Rindge, 1♀ (AMNH); 32 km SE Flagstaff, 28-VII-1975, Menke & Pulawski, 1♀ (USNM). COLORADO: Archuleta Co., Lower Piedra campground, 1.6 km N Piedra, 2195 m, 17-VI-1981, S. A. Teale, 2♂, 2♀ (UK); same as preceding but 5-VI-1986, JKG #377, 1♀ (ANSP); Mesa Co., Colorado National Monument, 18-V-1962, McCoy and Vogel, 1♂, det. *coconino* by S. Teale, (UCM); same but Fruita Entrance, 4700 ft (1433 m), 16-V-1985, on *Equisetum*, M. Weismann, 1♀ (UCM); Montezuma Co., Cortez, 1890 m, 22-V-1925, collector unknown, 3♂, 1♀ (USNM); 12km E Cortez on Co. Rd. 34, T36n, R14W, 19, 1981m, 6-VI-1986, JKG #379, 2♀ (ANSP). NEVADA: White Pine Co., Wheeler Peak vicinity, 12.9 km W, 2.4 km N of Baker, 2682 m, VI-13-1986, JKG #396, 1♀ (ANSP). UTAH: Cache Co., Logan Canyon, 1463 m (4800 ft), 30-VI-1942, CPA, 1♀ (USNM); Garfield Co., Blue Spruce Campground, 18 mi N Escalante, 2438 m, 29-VII-1965, F. P. & M. Rindge, 1♀ (AMNH); Red Canyon, 19 km SE Panguitch, 2195 m (7200 ft), 1-VIII-1965, F. P. & M. Rindge, 2♀ (AMNH); Starr Springs campground, Henry Mountains, 24-V-1978, Baumann et al., 4♂, 3♀ (BYU); Garfield/Kane Cos., Bryce Canyon, 14-VIII-1949, N. Cricknar, 1♀ (USNM); Grand Co., 16 km SE Moab, 30-V-1974, Knowlton and Hanson, 1♂, 1♀ (USU); Negro Bill Creek, Hwy. 128, Jct. Colorado River, 23-VI-1982, Baumann & Clark, 1♀ (BYU); Iron Co., pass on UT Hwy. #20, nr. Burnt Peak, 16.4 km E US Hwy. #15, 2408 m, 10-VI-1986, JKG #390, 2♂ (JKG, UMAA); Juab Co., Eureka, 30-VI-1911, T. Spalding, 1♂, paratype of *spaldingi*, (ANSP); as preceding except coll. 26-V and 11-VI-1921, 3♂, 2♀, not paratypes (ANSP); Kane Co., 11.6 km NE Cane Beds (AZ), 1646 m, pupae coll. 1-V-1986 at base of rock ledge, male emerged 12-V, JKG #368, 1♂, (JKG); Coral Pink Sand Dunes State Park, 1829 m (6000 ft), no date, C. v. Nidek, 1♀ (ZMUA); Glendale, Circle VH Ranch, 23-VI-1941, Sperry, 2♂, 1♀ (USNM); Kane Co., Navajo Lake, (2754 m), 21-VI-1949, W. Lange, 2♀ (UCD); Millard Co., Hot Springs, 12–13-V-1979, W. P. Nye, 3♂, 2♀ (USU); Maple Grove Forest Service Camp, 2012 m, 13-VI-1976, GWB, CWY, 1♀ v (USU); 6.4 km W Meadow, 19-V-1979, D. Zeeman 1♂, 2♀ (USU); Oak Creek, 5.3 km SE Oak City, 1707 m (5600 ft), 12-VI-1976, GWB, CWY #1, 1♀ (UK); Piute Co., Tushar Mountains, City Creek Campground, 10 km NW Junction, 2320m, 30-VI-1991, JKG #528, 2♀ (ANSP); Salt Lake Co., Salt Lake City, 18-IX-1974, light trap, Knowlton & Stephens, 1♀ (USU);

San Juan Co., Bluff, 28-IV-1935, B. E. & H. D. Rees, 1♂ (USNM); Devils Canyon campground, 18 km SW Monticello on US Hwy. #191, 2164 m, 6-VI-1986 evening, JKG #380, 4♂, 1♀ (AMNH, UK); Green Water Spring, 13-V-1961, W. Westman, 1♀ (BYU); La Sal Mts., Brumley Ridge, 6.4 km W, 19.3 km N La Sal, 2414 m, 7-VI-1986, JKG #384, 1♂, 1♀ (ANSP); Pack Creek Picnic Area, Manti La Sal National Forest, La Sal Mountains, (1951 m), 23-V-1978, R. Baumann, 1♀ (BYU); same but 1-VI-1982, Baumann, Clark and Mower, 1♂ (BYU); White Canyon, Natural Bridges National Monument, 27 June 1935, Brues, 1♂ (USNM); Tooele Co., Cedar Mountains (S end), 13-V-1954, H. Cott, 2♀ (UMAA); Little Valley Creek and Campground, Sheeprock Mountains, 14-VI-1980, Vernon and Baumann, 1♀ (BYU); Stansbury Mountains, Johnson Pass, 11-VI-1955, H. Cott, 3♀ (CAS); Stockton, 11-V-1913, T. Spalding, 2♂, paratypes of *spaldingi* (ANSP); same as preceding but 26-V and 19-VI, 1914, 2♀ (MCZ); same as preceding but 14-V-1913, 1♀ (UMAA); Utah Co., Goshen Ponds, E of Goshen, 23-V-1980, R. W. Baumann, 1♂ (BYU); 241 N 650 E Orem, 18-V-1980, E. Allen, 1♂ (BYU); Provo, 24-V-1912, T. Spalding, 5♂, paratypes of *spaldingi* (ANSP); Provo environs, 19-V-1936, D. E. Hardy, 1♂ (USNM); Utah Lake, west side, V.M. Tanner, 1♂, 1♀ (BYU); same but south shore, 26-V-1979, J. Griffiths, 1♀ (BYU); Washington Co., 6.9 km W Central, 1859 m, 29-VI-1986, JKG #365, 1♂, 2♀ (UK); same as preceding but reared from larvae in soil under *Cowania stansburyana*, adults emerged by V-9, 2♀ (ANSP); NW Leeds, 20-V-1963, at light, W. J. Hanson, 1♂, 1♀ (USU); Leeds Canyon, Oak Grove camp, 5-VI-1964, at light, 1♂ (USU); as preceding but coll. 14-VI-1978, G. F. Knowlton, 1♂, 5♀ (USU); 6.4 km NE Veyo, Baker Dam Reservoir, 1494 m, 29-IV-1986, JKG #364, 1♂ (UK).

Discussion.—The apices of the dorsal lobes of the male ninth tergum in *Tipula kaibabensis* show some variation in shape, even among individuals within a population. The apex may be acute and turned ventrally, or of irregular shape without a strongly acute point, or nearly truncate (Figs. 298, 300, 301).

Certain aspects of Alexander's descriptions and illustrations of *kaibabensis* (Alexander 1946a: fig. 7) are inaccurate or misleading, according to the specimens I examined. The ventral lobes of the ninth tergum are not darkened as shown by him, his figure of the inner dististyle shows a mixture

of setae from both the mesal and lateral surfaces, and the shape of the outer dististyle and shortened setae of the eighth sternum are not as illustrated.

Males of *kaibabensis* are likely to be confused only with other species in the *kaibabensis* species group (notwithstanding the error by Dietz in including individuals of *kaibabensis* among the type series of *spaldingi*). *Tipula kaibabensis* and *dimidiata* are particularly similar overall, but males can be easily differentiated by reference to the membranous lobe of the eighth sternum; other features distinguishing *kaibabensis* and *dimidiata* are listed in the corresponding section for *dimidiata*.

Females of *kaibabensis* are unlikely to be confused with any other *Eremotipula* species. The darkened, abruptly expanded inner ridges of the 8S are distinctive, and the wing pattern, when well developed pale areas are present, can only be confused with *mitrata*.

Relationships.—*Tipula kaibabensis* is the probable sister species of *dimidiata*. Further comments regarding the characters supporting this conclusion can be found under the "Relationships" section of *dimidiata* and the discussion of the phylogenetic analysis.

Geographic distribution.—Northern Arizona, east central Nevada, Utah, to western Colorado (Fig. 297).

Seasonal distribution.—Late April to mid August. A single record from Salt Lake City from September 18.

Habitat.—*Tipula kaibabensis* is most commonly found in pinyon pine-juniper communities (= Great Basin Conifer Woodland, Brown 1982a; Lower Transition Zone) at elevations ranging from 1433 to 2438 m. Common understory vegetation found at these sites includes *Artemisia tridentata* and *Cowania mexicana*. Occasional subdominants include shrubby oaks (*Quercus* sp.) and *Pinus ponderosa*. Alexander collected the type series on the Kaibab Plateau, Arizona, at about the highest elevation known for this species (2437 m). He recorded the flies as among "western yellow pine, white fir, oak and New Mexican locust, *Robinia neomexicana*" (Alexander 1946a: 487).

The species has been reared from larvae collected in soil under *Cowania stansburyana* in late April in Washington Co., Utah, and from pupae at the base of a rocky slope, in sandy soil under a 2.5 cm layer of oak leaves in early May, in Kane Co., Utah (Gelhaus, field notes).

The biproducta Species Group

This species group includes *biproducta* and *spinosa*. Synapomorphies of the two species are given in Figs. 29 and 34.

Tipula (Eremotipula) biproducta Alexander

Tipula (Lunatipula) biproducta Alexander 1947: 69–70; Alexander 1965b: 35, cat.; Alexander 1967: 25–26, fig. 82 (male 9T, ID, OD, apex of basistyle, 8S), key; Theischinger & Theowald 1981: 10, cat.

Diagnosis.—*Male*: Posterior margin of BS produced into huge, curved horn, nearly equal in length to outer basal lobe of ID (Fig. 309), apex of horn subacute (Fig. 310); membranous lobe between 8s and 9s elongate, subconical (Fig. 313). *Female*: Unknown (allotype female identity in doubt, see discussion).

Description.—Based on holotype male and some measurements from original description of Alexander (1947, in quotations); allotype female identity in doubt. *Length*: Male “about 17 mm”; female 21 mm (“about 21 mm”). *Head*: Vertex and postgena yellowish brown, pruinose. Antennal length: male “about 5 mm”. *Thorax*: Overall yellowish brown, pruinose. Presutural scutum with two pairs of scarcely contrasting, light brown stripes; remainder of notum pruinose. *Legs*: Femoral rings indistinct. Apices of tibiae slightly darkened. *Wings*: Male 16.0 mm long (“15.5 mm”); 4.0 mm wide. Overall light brown; stigma and spot at end of Sc brown. Pale area around stigma and extending as band along cord to cell m_4 . Darker line along Cu. (female allotype with pale streaks along A_1 , with much of cells r , r_5 , m and m_4 pale). *Abdomen*: Sublateral markings on terga light brown and small, median markings scarcely visible (“lateral stripes represented by darker but still smaller spots; best indicated on the posterior ring of tergite two and on basal positions of tergites three to five . . .”). *Hypopygium*: (from slide mounted specimen): *Ninth tergum*: Ratio of length 9T/BS not measurable. Dorsal lobes divergent, each moderately long, slightly longer than wide, apex acute and curved ventrad (Fig. 307). Mesal margin of each lobe irregular, with some distinct teeth. STP elongate, ratio of length STP/9T not measurable, a strong dorsal ridge extending along most of process, translucent in apical third, dorsal margin of STP deeply lacinate; cuticle not reticulate, even at 400x magnification. Shelf of ventral

plate roughly triangular, margin irregular, surface smooth and flat, with indistinct lobes (Fig. 308), only partially concealed by dorsal lobes. *Ninth sternum* (+ *basistyle*): Dorsomedial margin not discernible. Entire posterior corner of BS produced into huge, curved horn (Fig. 309), slightly smaller than outer basal lobe of ID, without setae on apical half, apex subacute (Fig. 310). No lobe near basistylar suture. Ventral lobe of A9S slightly expanded at base, scarcely extended distally (Fig. 310); setae on ventral lobe mostly broken off on holotype, but remaining setae short, pale, not noticeably thickened. *Outer dististyle*: Posterodorsal margin apparently straight, anterior extension elongate. *Inner dististyle*: Ventral surface of upper beak with many ridges. Lower beak with indistinct ridges, apex truncate. Crest (Fig. 311) pale, dorsal margin concave and serrulate, with rounded lobe posteriorly; scattered spinules basally. OBL a flattened blade of medium-length, L/W = 1.7, dorsal edge curled laterally, L/W = 1.7, apex truncate. *Adminiculum*: Apical half strongly bent posteriorly. Lateral plates not greatly developed, each terminating basally in a sharp, recurved hook (Fig. 312). Dorsal lobes separated, apparently divergent (not clearly visible from specimen), each apex strongly bent and boot-shaped, surface smooth. Median lobe strongly separated from dorsal lobes, extended posteriorly into a pale blade; posterior margin of median lobe with an upper spine and a lower bifurcating spine. *Eighth sternum*: General shape not discernible. Anterior margin and posterior sclerotized margin distorted. Membranous apex apparently with a thick band of setae, probably not divided medially, each end of band with sclerotized knob set with many setae, sclerotization extending as medial bar. Membranous lobe pale (Fig. 313), apparently flat, nearly 2x as long as wide, covered with spinules (Fig. 314), area around base of lobe bare and tuberculate, base of lobe clearly delimited.

Specimens examined.—*Type material*: Holotype ♂ (USNM): CALIFORNIA: San Diego Co., Borego, 21-VI-1944, G. Sperry. Allotype ♀ (USNM): topotypic and on same pin as holotype. The right antenna, left wing, one mesothoracic leg and abdomen beyond segment V of the ♂ holotype are all mounted on a microscope slide. The slide is labeled similarly to pinned specimen but also includes “HOLOTYPE 8474”. The holotype lacks the left antenna beyond flagellomere

VIII and the right prothoracic leg. The condition of the slide mounted genitalia is generally good, although the eighth sternum is severely distorted. The right wing and left antenna of the allotype ♀ are mounted on a separate microscope slide.

Discussion.—The female specimen pinned with the holotype male differs significantly in coloration, particularly in regards to wing pattern. Both specimens are on the same pin which is a common practice for denoting a mating pair, but it is not unusual to find two or three males or females on the same pin among material in the Alexander collection, some of these collected by Sperry or Alexander. Therefore, the fact that the holotype and allotype of *biproducta* are on the same pin is not a good indication that these flies were collected mating, or that they are even conspecific. In this case, the differences in coloration between the two specimens indicates that the female specimen is not conspecific with the male of *biproducta*.

Males of *Tipula biproducta* can be easily recognized by reference to the huge, elongate basistylar horns, a unique feature in the subgenus *Eremotipula*.

Relationships.—*Tipula biproducta* and *spinosa* share many synapomorphies, and are obviously closely related species. Further comments regarding the relationships of *biproducta* can be found in the "Relationships" section of *spinosa*.

Geographic distribution.—Southern California (Fig. 315). Alexander (1947) mentions that the type specimens were collected from the "Painted Desert", although this is not written on the locality labels.

Seasonal distribution.—The two specimens were collected on April 21.

Habitat.—There are no associated data with the specimens regarding the habitat where they were collected. The type locality, Borego (= Borrego Springs?), is located near the western boundary of the Sonoran Desert (Lower Colorado Valley subdivision, Turner & Brown 1982) and is the driest region of this desert. Common vegetation in this area includes creosote bush (*Larrea tridentata*), brittlebush (*Encelia farinosa*), *Agave deserti*, ocotillo (*Fouquieria splendens*) and *Opuntia* spp. I visited this area on April 22–23, 1986, but was unsuccessful at finding any *Tipula* in the Borrego Valley (about 235 m elevation).

Tipula (Eremotipula) spinosa, new species

Diagnosis.—*Male*: Posterodorsal edge of BS thickened, rounded and turned slightly inward; outer basal lobe of ID of moderate length, with free portion a narrow blade with digitiform apex (Fig. 319); median lobe of adminiculum bent with two spines; membranous lobe between 8S and 9S of moderate length, subconical and darkened, lobe visible in gap between sternal setae (Fig. 2). *Female*: Unknown.

Description.—*Length*: Male 15–16 mm. *Head*: Vertex and postgena dark brownish-gray to reddish-brown; irregular orange patches sublaterally on occiput. Antennal length: male 3–4 mm. *Thorax*: Overall brown or dark reddish-brown, pruinose. Presutural scutum with two pairs of narrow, dark brown longitudinal stripes, widest anteriorly. *Legs*: Femoral rings dark brown and distinct. Apices of tibiae slightly darkened. *Wing*: Male 13 mm long; 3 mm wide. Overall light brown (Riverside Co. male slightly darker); stigma brown to dark brown. Pale area surrounding stigma, extending as band along cord to discal cell and proximal sections of cells m_3 and m_4 , also pale streaks along vein A_1 and in cell a_1 . *Abdomen*: Mottled yellowish brown and brown, or evenly yellowish brown, shiny. Terga 2–6 with medial and sublateral dark brown spots. *Hypopygium* (Fig. 2): *Ninth tergum*: Ratio of length 9T/BS = 0.3–0.4. Dorsal lobes subparallel (Fig. 316), each moderately long, as long as wide, narrowing to subacute to acute apex; margin irregular, with some distinct teeth present. STP elongate, ratio of length STP/9T = 0.7–0.8, mostly compressed, a strong dorsal ridge extending along most of STP; sclerotized in basal third, narrowed and translucent apically. Dorsal margin of STP deeply lacinate along apical half, and continuing around apex. Cuticle of STP faintly reticulate near base, distally plicate. Ventral surface of shelf reticulate to rugose, margin entire. Ventral lobes parallel, only bases concealed beneath dorsal lobes (Fig. 317); each lobe elongate, narrow, and flattened. *Ninth sternum* (+ basistyle): Dorsomedial margin of BS entire, without produced area opposite sp1. Dorsolateral margin of BS opposite posterior condyle of ID produced into a short, strongly sclerotized, medial curved lobe. Ventral lobe of A9S with short, thickened setae on small knob; setae mostly directed ventrad (Fig. 318). *Outer dististyle*: Posterodorsal margin slightly concave, long anterior

extension (Fig. 2). *Inner dististyle*: Ventral surface of upper beak with weak ridges. Lower beak with truncate apex. Crest pale (Fig. 319), slight gap between crest and beak, upper margin slightly concave and serrulate, with rounded lobe posteriorly; scattered spinules basally. OBL a narrow blade of medium length, $L/W = 1.8-2.0$, directed posteriorly and dorsal margin curved laterally near apex, a strong ridge medially from near base to near apex, narrowed slightly near midlength, apical one-fourth digitiform. *Adminiculum*: Apical half strongly bent posteriorly. Lateral plates scarcely developed but each ending basally in a small recurved hook (Fig. 323). Dorsal lobes fused anteriorly but divergent at apex, each apex mucronate and smooth (Fig. 322). Median lobe widely separated from dorsal lobes, extended posteriorly with two spines on margin. Laterally, near base, median lobe with perpendicular, greatly expanded, rounded ridge. *Eighth sternum*: Posterior (sclerotized) margin concave. Membranous apex with band of long setae, band interrupted medially but widened laterally with thin sclerite at either end. Setae with rounded carinae; length of setae about equal to length of eighth sternum. Membranous lobe darkened, subconical, externally visible (Fig. 2; similar to that of *pellucida*), about 2.5x as long as wide (2.0x as seen externally); lobe covered with small denticles (Fig. 320), surrounding area bare, tuberculate and slightly sclerotized.

Specimens examined.—*Type material*: Holotype ♂ (KU): CALIFORNIA: Riverside Co., 27.5 km SW Palm Desert on CA. Hwy. #74, T7S, R5E, S9, elev. 1250 m, IV-21- 1986, at light, J.K. Gelhaus #344. Paratype: 1 ♂, CALIFORNIA: Inyo Co., 9 mi W Lone Pine, VI-15- 1964, J. S. Buckett (UCD). Holotype in good condition, with legs and antennae intact. Genitalia of both holotype and paratype stored in glycerin in vials attached to respective pins.

Etymology.—The species is named for the distinctive spines on the adminiculum, both at the base of the lateral plate and the bifid spines on the median lobe.

Discussion.—The specimen from Riverside Co. is darker overall in wing and body coloration than the specimen from Inyo Co.

Males of *Tipula spinosa* are distinctive and not likely to be confused with other species as noted in the key. In addition, the outer basal lobe of the inner dististyle in *spinosa* is generally similar to

that of *sinistra*, but these species differ in the dorsal and ventral lobes of the 9T and wing coloration. Also, the membranous lobe between the eighth and ninth sterna in *spinosa* is more extended and slightly sclerotized, unlike that of *sinistra*. Both *spinosa* and *pellucida* have similar membranous lobes, but differ in most other characters, including the structure of the microtrichia on the membranous lobe.

Relationships.—Clearly *Tipula spinosa* and *biproduca* are closely related based on the possession of five synapomorphies, four of these innovations of the male adminiculum, including a recurved spine at the base of each lateral plate and the posterior margin of the median lobe with two or three spines. Also, the membranous lobe between the eighth and ninth sterna in both species shows modification of the microtrichia: in *biproduca*, these are thickened spinules, and in *spinosa*, they are denticulate.

Geographic distribution.—Southern California (Fig. 315). The two known localities are located at the northern and southern edges of the Mojave Desert.

Seasonal distribution.—The more southern male was collected on April 15, and the northern one two months later, June 15.

Habitat.—The two specimens were collected in widely separated locations and probably quite different vegetational communities. I collected the Riverside Co. specimen in dense chamise (*Adenostoma* spp.) and *Ceanothus* sp. chaparral in the Santa Rosa Mountains at 1250 m elevation. No habitat data were associated with the Inyo Co. specimen, the locality probably lies within the sagebrush steppe or juniper-pinyon pine woodland zones.

The sinistra Species Group

This species group includes *middlekauffi*, *sinistra* and *woodi*. Synapomorphies of the three species are given in Fig. 34.

Tipula (Eremotipula) woodi Alexander

Tipula (Lunatipula) woodi Alexander 1948: 34–36, fig. 12 (9T, ID, OD); Alexander 1965b: 40, cat.; Theischinger & Theowald 1981: 49, cat.

Diagnosis.—Wing evenly grayish brown, with *c* and *sc* cells strongly yellowed, no pale area

along cord. *Male*: Dorsal lobes of 9T widely separated, divergent, with crenulate margin and STP elongate (Fig. 324); distinct ridge along outer basal lobe of ID, apex of lobe truncate (Fig. 327); setae on ventral lobe of A9S not thickened or short (Fig. 326); setae on apex of 8S in sparse band with membranous lobe of eighth sternum easily visible, flattened and linguiform (Fig. 330). *Female*: Each inner ridge of 8S as in Fig. 353, each hypogynial valve broadest at base.

Description.—*Length*: Male 18–21 mm; female 23–27 mm. *Head*: Vertex and postgena yellowish brown to brownish gray, densely pruinose. Antennal length: Male 4–5 mm, female 3 mm. *Thorax*: Overall yellowish to reddish brown (specimens from Nevada grayish brown), densely pruinose. Presutural scutum usually with two pairs of reddish brown to brown stripes, sometimes absent or indistinct; area between inner stripes yellowish, reddish to grayish brown and lightly pruinose. *Legs*: Femoral rings brown, distinct to indistinct. *Wing*: Male 16–18 mm long, 4 mm wide; female 16–19 mm long, 4–5 mm wide. Overall light grayish brown, without pale area along cord region; stigma usually scarcely darker. Cells *c* and *sc* strongly yellowed reaching and including stigma, sometimes faint yellow band along CuA. *Abdomen*: Bright yellowish brown to dark reddish brown in males, shiny. Male terga 2–5 with light brown, dorsal line (often absent) and brown, sublateral ones nearly continuous. Females from Utah yellowish brown with broad irregular grayish brown sublateral markings, these nearly contiguous, lateral border pale and contrasting, middorsal markings brown, small, not contiguous. Female from Nevada with abdomen dark grayish brown, with submedial irregular reddish markings; sublateral markings dark brown, semicircular, not contiguous, with lateral pale border, middorsal markings dark brown and nearly contiguous. Marginal setae of terga I light to dark, 2–4× length of other setae on tergum (shorter than setae on venter) in males and some females, other females with typical short black setae. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.6. Dorsal lobes divergent (Fig. 324), each small, twice as broad at base as long, apex subacute to rounded; margins irregularly toothed and darkened, each lobe connected ventrally to STP by a ridge. STP elongate, ratio of length STP/9T = 0.6–0.8, only slightly compressed, a slight ridge extending from base to midlength;

apical fourth of STP pale and slightly downturned, dorsal margin smooth. Reticulate cuticle of STP near base extending to ventral lobe. Ventral lobes partially visible from above, slightly convergent (Fig. 325); each lobe thick, wide, with truncate apex, extending from broad, flat plate. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of BS not produced opposite attachment of spl. Dorsolateral margin of BS opposite posterior condyle of ID slightly produced into flat, rounded lobe. Ventral lobes of A9S with setae pale, long, slender and directed ventrally (Fig. 326). *Outer dististyle*: Posterodorsal margin straight, anterior extension short, apex narrowly rounded. *Inner dististyle*: Ventral surface of upper beak with weak ridges, those of lower beak obsolete. Crest (Fig. 327) small, triangular, pale with scattered spinules, dorsal margin smooth; usually a narrow groove between crest and beak. OBL of medium length, L/W = 1.7–2.1, directed posteriorly and slightly bent laterally along posterior half, lobe only slightly expanded apically, with distinct lower ridge from base to apex, a few setae along edge of ridge but most scattered above ridge, apical margin of lobe subtruncate (dorsal aspect similar to *sinistra*, Fig. 345). *Adminiculum*: Lateral plates expanded throughout, scarcely narrowing at midlength opposite dorsal spine (Figs. 328, 329). Dorsal lobes flat, narrow, fused over median lobe, posterior margin truncate. Median lobe small, height one eighth that of total adminiculum, with slight dorsoventral carina on either side. *Eighth sternum*: Posterior (sclerotized) margin shallowly biconcave. Membranous apical region with sparse band (2–3 setae thick) of relatively short setae, band interrupted medially (Fig. 330); a small sclerite with few setae at either end of row. Setae with few carinae, usually lacking these entirely; setae less than two thirds length of sternum. Membranous lobe pale, linguiform, 1.3–2.3× as long as wide, with long, single (ungrouped) microtrichia. *Ovipositor*: Each inner ridge of 8S as in Fig. 353; each hypogynial valve broadest at base, apical half slightly to strongly narrowed. Vaginal apodeme (Fig. 362).

Specimens examined.—*Type material*: Holotype ♂ (USNM): **UTAH**: Utah Co., Spanish Fork, June 10, 1936, D. Elmo Hardy, holotype #8487. The type lacks all legs, and part of the abdomen is glued to the locality label. The left antenna, right wing, one leg and the hypopygium are mounted on a microscope slide similarly labeled to the

pinned specimen. The ninth tergum, adminiculum and eighth sternum are severely torn in the slide preparation.

Other specimens: **USA:** **NEVADA:** White Pine Co., 9.8 km E of McGill, along Timber Creek, 2430 m, 14-VI-1986, JKG #399, 2♂ (UK); Wheeler Peak vicinity, 12.9 km W, 2.4 km N of Baker, 2682 m, 13-VI-1986, JKG #396, 4♂, 1♀ (BYU, JKG). **UTAH:** Beaver Co., Mud Spring Ridge, 2.4 km E, 13 km N Manderfield, 2018 m, 11-VI-1986, JKG #393, 1♀ (ANSP); Millard Co., Oak Creek, 3.3 mi SE Oak City, 5600 ft (1707 m), 12-VI-1976, GWB #1,2, CWY, 6♂, 3♀ (ANSP, UK, USNM); Piute Co., Birch Creek Canyon, 1.6 km S, 3.2 km W of Circleville, 1963 m, 10-VI-1986, JKG #389, 1♂, 1♀ (UK).

Discussion.—The holotype male possesses a slightly smaller crest on the inner dististyle and has a shorter membranous lobe of the eighth sternum than seen in other specimens; neither the shape nor the size of either structure in the holotype appears to be an artifact of the slide-mounting process. The length/width ratio for the membranous lobe does vary within this species (1.2–2.3) with the holotype having an extreme condition (1.2).

The structure of the female hypogynial valve is variable in length and shape, although the base is consistently broader than the apex. Females of *woodi* can be recognized by a combination of features, including wing coloration (particularly lack of cord whitening and amber colored *c* and *sc* cells), shape of the hypogynial valve, inner ridge construction, and in some individuals, longer pale setae on abdominal tergum 1. In particular, the yellowed cells of the wing should separate this species from *madina* individuals with unmarked wings.

Geographic distribution.—Central Utah and eastern Nevada (Fig. 331).

Seasonal distribution.—All specimens were collected between June 10 and 14.

Habitat.—Habitat data are available for all collection sites, excluding the type locality. Except for shrubs of *Artemisia tridentata*, the dominant vegetation of the different localities varied from deciduous woodland to sagebrush steppe. Near Oak City, Utah, *woodi* was collected in the understory vegetation (mostly young oaks) of an oak woodland, with bordering open areas of *Artemisia* and *Chrysothamnus*. Also in Utah, in Birch Creek Canyon, this species was found in floodplain

shrubs of *Artemisia*, *Chrysothamnus*, *Cowania* and *Rhus*, with scattered junipers and clumps of *Quercus*. In Nevada, along Timber Creek, the habitat was entirely a steppe of *Artemisia tridentata* and *Purshia tridentata*. Teneral adults of *woodi* were collected in the morning among stunted *Artemisia* shrubs on a relatively open slope near Wheeler Peak, Nevada. Other vegetation consisted of scattered *Pinus monophylla*, tree-sized *Cercocarpus ledifolius* and bunch grasses.

Elevations of these localities range from almost 1400 m at the type locality in Utah to nearly 2700 m in Nevada.

Tipula (Eremotipula) middlekauffi Alexander

Tipula (Eremotipula) middlekauffi Alexander 1965a: 361–362; Alexander 1967: 26, fig. 90 (9T, ID, OD, A9S, 8S, sp2), key; Theischinger & Theowald 1981: 29, cat.

Diagnosis.—Legs dark brown with yellow ring preceding brown femoral ring; wing with CuA and m-cu conspicuously seamed with brown. *Male:* Hypopygium usually bent at nearly right angle to rest of abdomen; 9T with dorsal lobes broad, widely separated and with toothed margin (Fig. 332); ventral lobes thick, with acute apex (Fig. 333); membranous lobe linguiform, about 1.5x as long as wide (Fig. 338). Distributed in northeastern California. *Female:* Unknown.

Description.—Based on 2 males and description by Alexander (1965a), female unknown. *Length:* Male 17–20 mm. *Head:* Vertex and postgena yellowish brown, pruinose. Antennal length: male 5–6 mm. *Thorax:* Overall yellowish brown, pruinose. Presutural scutum with two pairs of elongate, indistinct, longitudinal stripes; area between inner stripes bright and scarcely pruinose. *Legs:* Legs dark brown (yellowish in most other species), yellowish band immediately preceding brown femoral ring. *Wing:* Male 17 mm long, 4 mm wide. Overall light brownish gray, cells *c* and *sc* strongly yellowed; stigma scarcely darker. Light yellowish band along CuA and m-cu. Pale band along cord and into cell *m*₄. Cells *r*, *m* and *m*₃ scarcely lighter than ground color. *Abdomen:* Terga 2–6 with sublateral, faint, brown lines. Posterior margin of tergum 1 with about ten elongate (length 4–5x that of other setae on tergum) light brown setae (as in Fig. 343). *Hypopygium:* *Ninth tergum:* Ratio of length 9T/BS = 0.6. Dorsal lobes

divergent (Fig. 332), triangular with toothed margin, each twice as broad at base as long, narrowing gradually to acute, slightly downturned apex; each lobe extended ventrally to STP as a ridge. STP elongate, ratio of length STP/9T = 0.6, compressed, greatly widened basally with dorsal ridge, abruptly narrowed and pale in apical fourth, dorsal margin slightly lacinate. Cuticle of STP near base reticulate, extending to ventral lobe. Ventral lobes partially visible from above, slightly convergent (Fig. 333); each lobe thick, with inner margin produced into a short, curved point, lobe extending from broad, flat plate. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of BS not produced opposite attachment of sp1. Dorso-lateral margin of BS opposite posterior condyle of ID slightly produced into flat, rounded lobe. Ventral lobe of A9S with most setae on ventral lobe short, thickened and yellowish brown (Fig. 335), setae directed laterad. *Outer dististyle*: Posterodorsal margin slightly concave, anterior extension short. *Inner dististyle*: Ventral surface of upper beak and apex of lower beak with weakly to well-developed ridges. Crest thickened, elongate (Fig. 336), extending to OBL with apex subtruncate, mostly membranous except for central band of sclerotization and scattered spinules throughout, dorsal margin serrulate; a slight groove between crest and beak. OBL of medium length, L/W = 1.8–2.0, directed posteriorly and rotated slightly laterally from base of ID, lobe of nearly uniform width throughout, with indistinct lower ridge from midlength to apex, dark setae scattered above ridge, apex rounded. *Adminiculum*: Similar to that of *sinistra* (Fig. 346). Lateral plates expanded throughout, emarginate dorsally at midlength opposite dorsal spine (Fig. 337). Dorsal lobes flat, narrow, fused over median lobe, posterior margin of each truncate. Median lobe small, height one eighth of total adminiculum, with slight dorsoventral carina on either side. *Eighth sternum*: Posterior (sclerotized) margin biconcave. Membranous apical region with setal band interrupted medially and laterally: two inner bands, each 2–3 setae thick; each lateral setal group on a sclerotized knob, sclerotization of knob extending medially. All carina on setae with rounded edges; setae over half length of sternum 8. Membranous lobe pale, linguiform (Fig. 338), about 1.5x as long as wide, with long, single (ungrouped) microtrichia.

Specimens examined.—*Type material*: Holotype ♂ (USNM): CALIFORNIA: Nevada Co., Truckee,

Agricultural Inspection Station, August 1948, Holotype 11,641. The holotype lacks most of the antennae, as well as all the legs, with part of an antenna, the right wing and the hypopygium mounted on a similarly labeled, microscope slide. The ninth tergum on the slide is compressed and torn, and the adminiculum is crushed. The type is in the Alexander collection (USNM), not in the California Insect Survey collection UCB as stated by Alexander (1967).

Other specimens: **USA: CALIFORNIA:** Nevada Co., Boca, (1737 m), 23-VI-1978, L. R. Bronson, 1♂ (UCD).

Discussion.—The illustrations provided by Alexander (1967: fig. 90) are misleading and require explanation. The ninth tergum is apparently a composite of both dorsal and ventral aspects. The setae on the appendage of the ninth sternum are not as short as illustrated, and the inner dististyle shows the mesal view. The structure marked “basistyle” must be sp2 of the basistyle and is of little diagnostic value.

Tipula middlekauffi is a distinctive species, and likely to be confused only with its sister species, *sinistra*. Both species share several characteristics not found elsewhere within *Eremotipula*, including a brown or yellowish seam along veins CuA and m-cu, dark brown legs with a yellow ring preceding the dark femoral ring and the male hypopygium deflected greatly dorsad. Males of *middlekauffi* may be distinguished from those of *sinistra* by characters listed in the key and diagnosis.

Geographic distribution.—Northeastern California (Fig. 331).

Seasonal distribution.—The collection date for the holotype is imprecise, simply labeled as “August”. The specimen from Boca, a town near the type locality and apparently at a similar elevation, was collected in late June.

Habitat.—No habitat data are associated with the two known specimens of *middlekauffi*. The dominant vegetation around Truckee, California, at an elevation near 1800 m, is either Jeffrey pine forest (often with an understory of *Artemisia tridentata* and *Purshia tridentata*) or *Artemisia-Agropyron* sagebrush steppe (Young, Evans & Major 1977).

Tipula (*Eremotipula*) *sinistra* Dietz

Tipula sinistra Dietz 1921: 8–9, fig. 9 (male 9T), key; Alexander 1945a: 414, loc., biol.; Alexander 1948: 30,

loc.; Alexander 1965b: 38, cat.; Theischinger & Theowald 1981: 40, cat.; Teale 1984: 34–35, redesc., key, loc., biol.

Tipula spernata Dietz 1921: 9–11, fig. 4 (male hypo., dor.), key; Alexander 1965b: 39, cat.; Theischinger & Theowald 1981: 41, cat. **NEW SYNONYMY.**

Diagnosis.—Legs usually dark brown with yellow ring preceding femoral ring (most distinct in males); wing with CuA and m-cu usually conspicuously seamed with brown. *Male*: hypopygium usually bent upward at nearly right angle to rest of abdomen; 9T with dorsal lobes widely separated, short and with toothed margin (Fig. 339); outer basal lobe of ID with distinct ridge extending entire length and setae only along edge of ridge (Fig. 344), apical portion bent laterally with apex truncate (Fig. 345); 8S with setal band interrupted medially, a short, pyramidal membranous lobe visible between rows (Fig. 350). *Female*: Each inner ridge of 8S as in Fig. 352.

Description.—*Length*: Male 14–19 mm; female 18–26 mm. *Head*: Vertex and postgena yellowish brown to brownish gray, pruinose anteriorly. Antennal length: male 4–5 mm, female 3–4 mm. *Thorax*: Overall yellowish brown, pruinose. Presutural scutum of males with two pairs of indistinct, longitudinal brown stripes or stripes absent; area between inner stripes scarcely pruinose, if stripes absent, median area sometimes appearing as a wide, longitudinal band, distinct from lateral areas of notum. Presutural scutum of females similar, but stripes generally brown and distinct; area between median stripes tan brown to brown, lateral stripes less distinct. *Legs*: Often brown (yellowish brown in most other species) with yellowish band immediately preceding brown femoral ring. *Wing*: Male 14–18 mm long, 3–5 mm wide; female 16–22 mm long, 4–5 mm wide. Overall light brown, yellowish in cells *c* and *sc*; stigma brown, and distinct brown band along CuA and m-cu (Fig. 446). Pale area around stigma, extending as band along cord, contiguous to pale areas in cells *r*, *m* and *m*₃, broad pale streaks encompassing vein A₁, inconspicuous streak in cell *a*₁. *Abdomen*: Male terga 2–6 with sublateral, faint, brown line, lightest on 2 and 5. Female terga with dark, sublateral patches, forming nearly continuous line, lateral borders pale, appearing as white line next to dark brown. Posterior margin of tergum 1 with about ten, long (length 4–6 × that of other setae on tergum) light brown setae. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS =

0.5–0.6. Dorsal lobes divergent (Fig. 339), widely separated, each small, basal width over twice length, apex subacute; margin irregularly toothed and darkened, each lobe connected ventrally to STP by a darkened ridge. STP elongate, ratio of length STP/9T = 0.6–0.8, compressed, with dorsal ridge extending entire length; basal three-fourths of STP sclerotized, remainder pale with serrate or lacinate margin. Cuticle of STP near base reticulate. Ventral surface of shelf smooth. Ventral lobes slightly exposed, convergent (Fig. 340), each lobe small, thick, with acute to nearly truncate apex. *Ninth sternum* (+ *basistyle*): Dorsomedial margin of BS sometimes produced opposite sp1. Dorso-lateral margin of BS opposite posterior condyle of ID moderately produced posteriorly into flat, rounded lobe. Ventral lobes of A9S (Fig. 342) with numerous, straight, thickened, reddish brown, laterally directed setae; marginal setae thinner, longer and pale. *Outer dististyle*: Posterodorsal margin slightly emarginate to straight, with short anterior extension (Fig. 349). *Inner dististyle*: Ventral surface of upper beak with weakly developed ridges, lower beak smooth; dark, thin ridge on lateral surface of lower edge of upper beak. Crest small, narrow, triangular (Fig. 344), with scattered spinules and margin entire. OBL of medium length, L/W = 1.5–1.9, directed posteriorly and bent slightly laterally along posterior half (Fig. 345), of nearly uniform width beyond base, with distinct medial ridge from base to truncate apex, setae in row along ridge. *Adminiculum*: Lateral plates greatly expanded throughout, emarginate dorsally with short lateral point at midlength opposite dorsal spine (Fig. 347). Dorsal lobes flat, smooth, perpendicular to median lobe, apex of each nearly truncate, but with lateral point. Median lobe small, height about one seventh of total adminiculum (Fig. 346), slightly thickened, with short beak; a dorsoventral carina extending from beak on either side. *Eighth sternum*: Posterior (sclerotized) edge biconcave with a darkened medial spot (Fig. 348). Membranous apical region with setal band interrupted medially and laterally: two inner rows, each 2–3 setae wide; each lateral setal group on partially sclerotized knob. Carinae on setae set with acute points; setae three-fourths length of 8S. Membranous lobe pale, nearly three-sided, about twice as wide as long, immediately posteromedial to setae and exposed between setal rows (Fig. 350), with microtrichia in groups of 2–3 (Fig. 351). *Ovipositor*: Each inner ridge of 8S of moderate height and length, 0.9–1.1 mm long,

light brown (except pale dorsal edge) (Figs. 352, 354–358); appressed against floor of 8S in uncleared specimens. Vaginal apodeme elongate, expanded into diamond shape dorsally, remainder long and slender (Figs. 363–367).

Specimens examined.—*Type material:* *Tipula sinistra* Dietz. Holotype ♂ (ANSP): Northwestern Colorado, county unknown, July 11, 1911, Holotype #6397. Dietz gives similar locality data in the original description but cites a collection date of August 11, 1911, adding that E. J. Oslar was the collector. I consider the date of collection on the label as correct. The holotype is in fair condition, with the apical half of the left antenna missing and the abdomen broken into three pieces: one piece glued to the thorax, the other two including the hypopygium mounted on points. The left front leg is the only leg remaining.

Tipula spermata Dietz. Holotype ♂ (ANSP): COLORADO: Park Co., South Park, June 23, 1916, Holotype #6398. The holotype has most of the left antenna missing, with four pieces of legs, both wings and the abdomen glued to the body. Paratype: 1♂, COLORADO: Clear Creek Co., Clear Creek, June 11, 1916, E. J. Oslar (ANSP).

Other specimens: 55♂, 12♀. **CANADA:** ALBERTA: Coleman, 1400 m, 25–31-VII-1987, C. & A. v. Nidek, 4♀ (ZMUA). BRITISH COLUMBIA: Michel, 17–24-VII, Garrett, 1♂, 2♀ (UMAA); Johnstone Creek Provincial Park, east of Osoyoos, 16-VIII-1975, W. H. Lange, 1♂, 2♀ (UCD); Peachland, 7-VIII-1912, 1f (ANSP). **USA:** ARIZONA: Coconino Co., 11 km E Jacob Lake, 2072 m, 23-VII-1965, F. P. & M. Rindge, 1♀ (AMNH); North Rim, VIII-1949, N. Cricknar, 1♂ (USNM). CALIFORNIA: Siskiyou Co., Mount Shasta, east, 6000 ft (1829 m), 17-VII-1939, M. Lane, 1♂ (USNM). COLORADO: Boulder Co., Camp Dick, 6 mi N Ward, 8600 ft (2621 m), 9-VII-1974, GWB #12, CWY, 1♂ (UK); Ward, (2820 m), 11-VII-1949, L. D. Beamer, 1♂, 1♀ (UMAA); Grand Co., St. Louis Creek Camp, 5 km SW Fraser, 8800 ft (2682 m), 30-VII-1967, F. P. & M. Rindge, 1♂, 3♀ (AMNH); also 8 km SW Fraser, 29-VII-1967, 1♀ (AMNH); Tabernash Campground, 5 mi S of Granby, 8560 ft (2609 m), 19-VII-1981, GWB #7, SAT, 2♂, 1♀ (UK); Gunnison Co., Gothic, (2896 m), 14-VII-1952, E. Pruitt #20, 1♂ (UK); La Plata Co., Electra Lake, 8400 ft (2560 m), 28-VI & 1-VII, 1917, 3♂ (AMNH); Larimer Co., Pole Hill, 40°21'42"N, 105°25'58"W, 2590m, 19-VII-1982, T. McCabe, 2♀ (ANSP); Rocky Mountain National Park, Glacier Basin, 8350 ft (2545 m),

23-VII-1941, CPA, 1♂ (USNM); Mesa Co., Glade Park, (2057 m), 8-VII-1953, A. B. Gurney, 2♂ (USNM); Summit Co., Blue River Campground, 12 km NW of Silverthorne, 2585 m, 5-VIII-1981, at light, SAT, 4♂, 2♀ (UK). IDAHO: Bannock Co., Mink Creek, Cherry Springs, 19-VI to 3-VIII, 1973, in oil trap, D. W. Shaw, 1♂ (UK); Fremont Co., 6.4 km SW Mack's Inn, 15-VII-1956, W. Barr, 1♀ (UIM). MONTANA: Glacier National Park, Rising Sun Campground, 27-VIII-1981, at light, P. Arnaud, Jr., 1♀ (CAS). NEVADA: Elko Co., Angel Creek campground, 13 km SW of Wells, 2134 m, 15-VI-1986, JKG #400, 10♂, 7♀ (JKG, UK, UMAA); Angel Lake vicinity, 18 km SW of Wells, 2499 m, 15–16-VI-1986, pupa in soil under *Artemisia tridentata*, male emerged 26-VI, JKG #401, 1♂ (JKG); White Pine Co., Lehman Creek Campground, 11.3 km W of Baker, 2286 m, 13-VI-1986, at light, J. K. & M. F. Gelhaus #395, 1♂ (UK); Wheeler Peak vicinity, 12.9 km W, 2.4 km N Baker, 2682m, 13-VI-1986, JKG #396, 1♀ (ANSP); 9.8 km E of McGill, along Timber Creek, 2430 m, 14-VI-1986, JKG #399, 2♂ (JKG, UK). OREGON: Hood River/Clackamas Cos., Mount Hood, 3000–6000 ft (914–1829 m), 25-VI-1925, E. C. Van Dyke, 1♂ (CAS); Malheur Co., Spring Creek, Blue Mountains, 3900ft (1189m), 20-VIII-1948, Baker, 1♀ (USNM). UTAH: Beaver Co., Beaver, in the mountains, 10-VII-1942, Knowlton (specimen not examined); Box Elder Co., Long Birch Creek at headwater springs, 16-VII-1980, at light, Baumann & Clark, 2♂, 1♀ (BYU); Willard Basin (16 mi SW Mantua), 6-VII-1956, G. Knowlton, 1♂ (UK); Willard Peak, 6-VII-1956, G. Knowlton, 1♂ (UK); Cache Co., Blacksmith Fork Canyon, 14–16-VII-1964, Malaise trap, W. Hanson, 2♀ (USU); Logan, 17-VII-1941, R. S. Roberts, 1♂ (USNM); Tony Grove Canyon, 7800 ft (2377 m), 10–16-VII-1975, in Malaise trap, Knowlton & Hanson, 1♂ (USU); Duchesne Co., Moosehorn Lake, Highway #150, Uinta Mountains (3169 m), 10-VIII-1978, at light, R. W. & W. Baumann, 1♂ (UK); Juab Co., Mount Nebo loop road, 3-VII-1972, W. Hanson, G. Knowlton, 1♀ (USU); Piute Co., Tushar Mountains, City Creek Campground, 10 km N Junction, 2320m, 1-VII-1991, JKG #528, 1♂ (ANSP); Rich Co., 5 km SW Garden City, US Hwy. 89, 2073 m, 26-VI-1988, GWB #1, 1♂ (UK); San Juan Co., Dalton Springs Campground, 8 km W Monticello, 2591m, 12–14-VII-1963, F. P. & M. Rindge, 3♀ (AMNH); Uintah Co., Uintah Canyon, 7-VIII-1980, Hanson & Knowlton, 1♂ (USU); Utah Co., Alpine Loop road, 25-VII-1973, W. Hanson,

1♀ (USU); Provo environs, H. Cott, 1♂ (BYU); Timpoooneke Campground, South Fork of American Fork River (2255 m), 12-VII-1978, R. W. Baumann, 1♂ (BYU). WYOMING: Carbon Co., Battle Creek Campground, near junction of highways #70 & 71, Sierra Madre Range, 7400 ft (2256 m), 19-VII-1982, J. P. & K. E. Donahue, 1♂ (LACM); Bottle Creek Campground, 7 mi SW Encampment, 8800 ft (2682 m), 1-5-VIII-1967, F. P. & M. Rindge, 2♂, 6♀ (AMNH); Elk Mountain, 2987 m, 20-VII-1978, R. Lavigne, 1♂ (UWL); Stratton Experimental Watershed, near Saratoga, 26-29-VI-1972, J. M. Schmid, 2♂, 1♀ (UK); Sublette Co., Sacajawea Campground, 39 km W of Big Piney, 2530 m, 27-28-VII-1986, JKG #414, A. Roig, 1♂, 3♀ (JKG); Teton Co., Moran, 24-VII-1938, 7-VIII-1941, G. H. & J. L. Sperry, 1♂, 1♀ (AMNH, USNM); Grand Teton National Park, Hidden Falls, 7000 ft (2134 m), 4-VII-1941, CPA, 1♂ (USNM); same but Jenny Lake, 6800 ft (2073 m), 1-VII-1941, CPA, 2♂ (USNM); same but Leigh Lake, 6780 ft (2067 m), 12-VII-1941, CPA, 2♂ (USNM); same but 0.5 mi E of University of Wyoming Research Station, 29-VII-1980, M. G. Pogue, 1♂, 1♀ (UWL); same but Teton Science School, near Kelly, 24-25-VII-1982, S. C. Williams, 2♂, 2♀ (CAS).

Discussion.—Dietz (1921) compared *spernata* with *sinistra* and listed four criteria for distinguishing these species: body size, thoracic markings and the structure of the “canthi” (= dorsal lobes of ninth tergum) and “inner apical appendages” (= inner dististyles). The differences in body size and coloration fall within the normal variation for *sinistra*, and although Dietz stated that the canthi of the two species differed, his descriptions of the canthi in both species are similar and I can see no specific differences between the two holotype specimens. The differences in the inner apical appendages he describes are even more puzzling. He states that the “evolved portion” (= crest?) is “inconspicuous” in *spernata* and “. . . conspicuous, large” in *sinistra*. The inner dististyles in the holotype of *sinistra* have the beaks pointing more or less upward, which allows the crest to be more easily seen; the dististyles in the holotype of *spernata* have the beaks drawn against the ninth tergum. Regardless of how the dististyles are positioned, the crests in both holotypes are alike in size and shape. In fact, the hypopygial structures of the two type specimens are alike in all important specific features, and I have no hesitation in considering the specimens conspecific.

Both *sinistra* and *spernata* were described in the same paper, with the original description of *sinistra* immediately preceding that of *spernata*. More importantly, *sinistra* has been recognized subsequently (e.g., Alexander 1945a, 1948), while *spernata* has not. Therefore, I consider *sinistra* as the valid name for the species.

Tipula sinistra varies somewhat in body coloration, with the wing pattern faintly expressed in some individuals, and the legs occasionally more yellowish brown instead of dark brown. The ventral lobes of the male ninth tergum sometime have the edges lightly rounded, although still appearing generally truncate.

Regarding specific determination, males of *Tipula sinistra* can only be confused with others in its species group, and can be distinguished using the characters listed in the key and diagnosis. The females can be recognized by the combination of the wing color pattern, long pale setae on tergum 1, the morphology and pigmentation of the 8S and the shape of the vaginal apodeme. The wing coloration, although only found in *middlekauffi* and *sinistra* in *Eremotipula*, is similar to that in some sympatric species of *Lunatipula*. The female terminalia of these *Lunatipula*, however, lack the subgeneric features of *Eremotipula* (e.g. sinuous border of hypogynial valve).

Relationships.—The wing pattern and leg coloration in *sinistra* and *middlekauffi* are unique within *Eremotipula*, and demonstrates a close relationship between these two species. Additional support for a sister-species relationship between these two is provided by two features of the membranous lobe of the eighth sternum, i.e., a faint sclerite on either side of the lobe, and a pyramidal shape (only slightly indicated in *middlekauffi*), as well as the lateral emargination of the adminiculum.

Geographic distribution.—Alberta and British Columbia, south to northern California and Arizona, west to Colorado and Wyoming (Fig. 368).

Seasonal distribution.—Mid June to mid August, with most records in July. *Tipula sinistra* can be found in flight later in the season than most species in the subgenus.

Habitat.—Alexander (1945a) recorded *Tipula sinistra* as occurring “among lodgepole pines” in the Teton Mountains of Wyoming. I have also collected this species in spruce, fir or pine forests. At nearly all of these localities, though, open areas of *Artemisia tridentata* were adjacent to the woods. I

have also collected *sinistra* at two localities in Nevada in steppe of *Artemisia tridentata* and *Purshia tridentata* at high elevations. Several pairs were found in copula around 4:00 PM (PDST) at Angel Creek, Nevada.

A single male pupa was collected in fine soil under a thin litter layer beneath *Artemisia tridentata* at Angel Lake, Nevada. The lake was situated in a basin near the summit of the Ruby Mountains, with patches of snow left on the nearby slopes.

Although *Tipula sinistra* has been found from about 1400 to 3200 m, nearly all records are above 2000 m, with many at high elevations above 2500 m. Moosehorn Lake, Utah (3169 m), is one of the highest localities inhabited by any species of *Eremotipula*.

The diversa Species Group

This species group includes *disspina*, *diversa*, *evalynae*, *leiocantlia*, *lyrifera* and *sackeni*. Synapomorphies of the six species are given in Figs. 21, 30.

Tipula (Eremotipula) disspina, new species

Diagnosis.—Thoracic notum with long, erect, light brown setae, similar to those on coxae, unlike shorter, darker, more appressed setae found in other species. Wing brownish gray, without paler streaks. **Male:** Elongate outer basal lobe of ID as in *diversa* group; basistylar spine lacking; OD broad and not extended anteriorly; ventral lobes of 9T truncate (Fig. 370); setal band of 8S divided at midlength, submedial setae extremely long and strongly curled (Fig. 374). **Female:** Unknown.

Description.—**Length:** Male 18 mm. **Head:** Overall yellowish brown, with pruinosity on vertex, postgena, and dorsally on rostrum near base. Antennal length: male 5 mm. **Thorax:** Overall yellowish brown, pruinose. Setae long and light brown (similar to those of coxae). Presutural scutum with two pairs of indistinct brown stripes; remainder of nota pruinose, with area between inner pair of stripes only slightly so. **Legs:** Femoral rings obsolete, no darkening at apices of tibia. **Wing:** Male 16 mm long; 4 mm wide. Overall light brownish gray. Stigma and cells *c* and *sc* strongly yellowed. No pale areas. **Abdomen:** Dark reddish brown (postmortem color change?). No darker markings. Setae on posterior margin of tergum 1 light brown, length over 3x that of other setae on

tergum. **Hypopygium:** *Ninth tergum:* Ratio of length 9T/BS = 0.5. Dorsal lobes moderately extended, nearly as long as wide, apices rounded and slightly divergent (Fig. 369), border irregular with several minute, but distinct teeth. STP elongate, ratio of length STP/9T = 0.8, compressed, with dorsal ridge on basal half; slightly downturned, narrowed in apical half. Basal third of STP sclerotized, remainder pale and membranous, with dorsal margin strongly laciniate. Ventral surface of shelf rugose anteriorly. Ventral lobes partially visible from above, lobes convergent (Fig. 370), with thick, nearly truncate upper portion and flat, rounded lower portion. *Ninth sternum (+ basistyle):* Dorsomedial margin of BS with small point opposite attachment of sp1. Dorsolateral margin of BS broadly truncate opposite posterior condyle of ID. Ventral lobes of A9S with numerous, thickened, short, reddish-brown setae, directed laterally. *Outer dististyle:* Style short, wide, without anterior extension, apex rounded and directed dorsad. *Inner dististyle:* Ventral surface of upper beak and dorsal surface of lower beak with several ridges. A pale carina along lower margin of upper beak, extending nearly to crest. Crest (Fig. 371) pale, low, dorsal margin straight, entire, with scattered spinules along base; a slight groove between crest and upper beak. OBL elongate, L/W = 2.7, directed posteriorly and dorsal margin curled laterally with respect to base of ID, with well-developed, longitudinal ridge; setae on ridge anteriorly, more scattered posteriorly on lobe. Apical region of OBL curled outwardly but not twisted completely, narrowing to truncate apex. *Adminiculum:* Dorsal spine far anterior to median lobe. Lateral plates with margin nearly straight and entire, narrowed slightly dorsally (Fig. 372); dorsal lobes narrow, spine-like, fused anteriorly (Fig. 373). Median lobe small but distinct, slightly produced dorsally, with long beak ventrally. *Eighth sternum:* Posterior (sclerotized) edge concave. Membranous apical region with broad band of long setae, band greatly expanded toward midlength, but narrowly interrupted along median line (Fig. 374); a narrow sclerite bearing many setae located at either end of band (Fig. 375). Medial setae extensively curled apically. Behind setae, a broad membranous lobe, about as long as wide, narrowed to apex, with single (ungrouped) microtrichia (Fig. 376).

Specimens examined.—*Type material:* Holotype ♂ (USNM): ARIZONA: Williams, 24.5, H. S.

Barber Collector. The specimen bears a label reading: "Tipula/pyramis/Doane/det Dietz" (red bordered label, probably in C. P. Alexander's handwriting). The specimen was found in Alexander's collection under the heading "Tipula pyramis Doane", together with a paratype of *pyramis*. The condition of the type specimen is generally good, with the left foreleg attached to the body, and three other legs glued to a card below the specimen. The thoracic notum has several cracks in the cuticle. I cleared the terminal half of the abdomen and placed it in glycerin in a genitalia vial on the same pin as the specimen.

Other specimens: None.

Etymology.—The specific epithet *dissipina* is derived from *dis-*, without, and *spina*, spine, and refers to the lack of a spine on the dorsal margin of the basistyle. All other members of the *diversa* species group possess this spine.

Relationships.—*Tipula dissipina* appears best supported as a member of the *diversa* species group, based on three derived features of the inner dististyle: similar crest shape, an elongate blade-like outer basal lobe and a dorsal ridge on the lobe with dark setae along it. An equally parsimonious solution relates *dissipina* to the *sinistra* and *biproducta* groups; see discussion of phylogenetic analyses. Clearly *dissipina* is the most basal species in the *diversa* group, as it lacks many apomorphic features characteristic of this group, including a glabrous membranous lobe of the eighth sternum, acute dorsal and rounded ventral lobes of the 9T, and the presence of an elongate basistylar spine. *Tipula dissipina* provides an important insight into the relationship of the highly apomorphic *diversa* group to other groups in *Eremotipula*, particularly the *sinistra* and *spinosa* groups. For example, the common possession of similarly shaped ventral lobes of the 9T and the broad membranous lobe between the eighth and ninth sterna in *dissipina* and the *sinistra* group indicates that the *diversa* and *sinistra* groups are probably sister groups.

Geographic distribution.—Central Arizona (Fig. 377).

Habitat.—No information on the habitat of *Tipula dissipina* appears on the collection label, but the area surrounding the type locality (Williams, Coconino Co., Arizona, 2056 m elevation) falls within the Montane Conifer Forest region (Pace & Brown 1982a), dominated by *Pinus ponderosa*, *Pseudotsuga menziesii* and *Abies concolor*.

The locality data with the holotype of *dissipina* agrees with that found on specimens of *Tipula dimidiata* in the USNM. It is likely that the specimens were collected together in the same habitat.

Tipula (Eremotipula) evalynae, new species

Tipula lyrifera: Alexander 1948: 27.

Diagnosis.—*Male*: Hypopygium as in *diversa* group, including elongate OBL (Fig. 381) and prominent basistylar spine (as in Fig. 427); OBL nearly straight and almost flattened, with anterior ridge sclerotized, well-developed and shelf-like and ventral lobes of A9S with long, straight pale setae, some lateral setae shorter and slightly thickened (Fig. 380). *Female*: Without brown, distinct thoracic stripes, lacking pale patch along vein Cu and in *m* cells on wing; ovipositor with elongate pale inner ridges of 8S and overall whitish 8S; pigmentation stripes reduced or absent; hypogynial valves with subacute apex. Found in Utah, northern Arizona and southern Nevada.

Description.—*Length*: Male 19–21 mm, female 20–27 mm. *Head*: Vertex and postgena yellowish brown to brownish gray, sometimes with sublateral yellowish patches on occiput. Antennal length: male 5–6 mm, female 3 mm. *Thorax*: Overall yellowish brown, pruinose. In males, presutural scutum with two pairs of parallel, longitudinal, sometimes indistinct, brown stripes, area between inner stripes sometimes yellowish brown, less pruinose and brighter, contrasting with remainder of thorax; median stripes in females not strongly contrasting with reddish-brown background coloration. *Legs*: Femoral rings light brown; apices of tibiae darkened. *Wing*: Male 16–18 mm long, 4 mm wide; female 14–20 mm long, 4–5 mm wide. Overall light yellowish-brown; stigma brown, color extending to end of Sc. Cells *c* and *sc* yellowish. Pale band extending from stigma along cord and into discal cell. *Abdomen*: Male terga 2–5 with indistinct, brown, sublateral markings; no dorsal markings. Female terga 2–7 with sublateral, brown to dark-brown, continuous line, lateral border pale; medially with faint brown line, or line absent. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5–0.6. Dorsal lobes subparallel, usually closely appressed to STP in dried specimens (Fig. 378), of moderate length, slightly wider at base than long; border only slightly roughened, apex subacute to

nearly diagonally truncate, rarely rounded. STP elongate, ratio of length STP/9T = 0.5–0.7, compressed, of nearly equal height throughout, abruptly narrowing subapically along ventral margin, apex nearly truncate. Dorsum of STP lightly sclerotized in basal half, pale distally with margin deeply lacinate; cuticle at base faintly reticulate. Ventral surface of shelf smooth. Ventral lobes mostly visible from above, slightly convergent (Fig. 379), each lobe broad, smooth, with rounded apical margin and ventral ridge near base. *Ninth sternum* (+ *basistyle*): Lateral margin as in Fig. 427. Dorsomedial margin of BS straight opposite sp1. Dorsolateral margin of BS greatly produced opposite posterior condyle of ID, with inwardly curved, elongate spine at apex (as in Fig. 427). Ventral lobes of A9S with mostly long, pale, erect setae (Fig. 380), some lateral setae reddish brown, shorter and slightly thickened. *Outer dististyle*: Posterodorsal margin nearly straight, anterior extension long. *Inner dististyle*: Ventral surface of upper beak with well-developed ridges, those of lower beak indistinct. Crest (Fig. 381) pale, low, subtriangular with spinules along base. OBL elongate, generally flattened, and straight, L/W = 2.7–3.2, directed posteriorly and dorsal margin curled 90° with respect to base of ID, of nearly uniform width beyond base of OBL, subapical region narrowed, sometimes abruptly, apex subacute and not curved or twisted; well-developed, sclerotized, shelf-like, longitudinal ridge on lateral surface, extending from base to midlength; dark setae in row along ridge. Posterior margin of ID dorsad of posterior condyle weakly convex. *Adminiculum*: Lateral plates basally expanded, emarginate dorsally nearly opposite dorsal spine with indistinct point (Fig. 382), each plate abruptly narrowed above point. Dorsal lobes basally fused, apices slightly separated and rounded, with parallel striae. Median lobe small (about one-eighth total height of adminiculum), with lateral carinae. A pair of indistinct vertical ridges flanking posterior margin below median lobe. *Eighth sternum*: Posterior (sclerotized) edge shallowly concave. Membranous apical region with broad band of long setae, mostly 7–8 setae thick, widest laterally and at midlength. Setae carinate; slightly over half length of 8S. Behind setae, a pale, glabrous, flattened membranous lobe, slightly wider than long, and apex rounded; surrounding area tuberculate

and bare of trichia and sclerites. *Ovipositor*: Cerci (Fig. 412). 8S mostly ivory, base brown. Each inner ridge of 8S elongate, pale and without pigmentation (Fig. 408), inner pigmentation stripes at most light brown and granular in pattern, outer stripes very faint or absent, lateral edge with shallow cavity anteriorly (opposite ridge). Vaginal apodeme broad subapically with edges roughened, an elongate attenuated tip dorsally.

Specimens examined.—*Type material*: Holotype ♂ (UK): УТАН: Piute Co., Circleville, elev. 1714 m, on bldg. wall, VII-25-1983, J. K. & E. B. Gelhaus #284. Paratypes: 18♂, 14♀. ARIZONA: Coconino Co., North Rim of Grand Canyon, 30-VII-1938, at lights, L. Schellbach, 1♂ (USNM); as preceding but VIII-1949, N. Cricknar, 3♂, 4♀ (USNM); as preceding but Kaibab Plateau, 8000 ft (2438 m), 17-VI-1942, CPA, 1♂, 1♀ (USNM); 7 mi E Jacob Lake, 2073 m (6800 ft), 6♂, 3♀ (AMNH). NEVADA: Clark Co., Spring Mountains, 64 km NW Las Vegas at NV Hwy. #156 & 158, 2440 m, 28-VI-1991, JKG #526, 2♂ (ANSP); as preceding but Kyle Canyon Campground, 7200 ft. (2190 m), 13-VII-1981, Baumann and Cox, 1♀ (BYU); as preceding but Lee Canyon, 40 km NW Las Vegas, 7500 ft (2286 m), 23-VII-1966, F. P. & M. Rindge, 1♂, 5♀ (AMNH). УТАН: Beaver Co., Beaver Canyon, 7200 ft (2195 m), 12-VII-1945, Knowlton, det. as *lyrifera* by CPA, 1♀ (USNM); Kane Co., Coral Pink Sand Dune State Park, (1829 m), 4-VI-1981, R. W. Baumann, 1♂ (BYU); Uintah Co., 4-VII-1937, G. E. Wallace, 1♂ (CMNH); unknown county (probably southwestern Utah), Kaibab Forest, 22-VI-1933, J. T. Howell, 1♂ (CAS).

Regarding the specimen from "Kaibab Forest, Utah", the Kaibab National Forest is presently located in northern Arizona, with the Dixie National Forest occurring in nearby southern Utah. I am not aware of a "Kaibab Forest" in Utah.

Etymology.—I name this species for my wife, Evalyn, in deep appreciation for all the support she has given me in my research.

Discussion.—Alexander (1948) identified a specimen from Beaver Canyon, Beaver Co., Utah, of *evalynae* as *lyrifera*. In fact, the specimen was part of his synoptic collection of western North American *Tipula*. *Tipula evalynae* can be easily separated from *lyrifera*, *diversa* and *sackeni* by examining the outer basal lobe in males. The outer basal lobe is straight, relatively short and without a lat-

erally curved apex in *evalyinae*. The corresponding lobe is longer, and bent or curved apically in the other three species.

Females of *evalyinae* are much more difficult to separate from known females of other members of the *diversa* group, particularly *leiocantha*. They can be separated from *lyrifera* by hypogynial valve and cerci shapes, and from *diversa* and *sackeni* by wing and body coloration and pattern as indicated in the key. I have not found clear differences for separating females of *leiocantha* from *evalyinae*, although the hypogynial valve tips appear to come to a more narrow, sharper point in *evalyinae* than in *leiocantha* in the limited number of specimens I was able to examine. The ranges of the two species are closely approximated but apparently separate.

Relationships.—Although a sister species relationship of *evalyinae* to *leiocantha* is not supported by the phylogenetic analyses, possible evidence and the taxonomic distinctions between the species are detailed in the corresponding section of *leiocantha*.

Geographic distribution.—Northeastern Utah southwestward to northern Arizona and southern Nevada (Fig. 377).

Seasonal distribution.—Early June to August.

Habitat.—I collected a male *Tipula evalyinae* and observed a few others in low fir branches on a steep slope in the Spring Mountains, Nevada. Other dominant vegetation included mature pine, junipers, Great Basin sagebrush, and curl-leaf mountain mahogany. Information on vegetation at some of the other known localities is available. Alexander (1946a: 28) states that the vegetation of the Kaibab Plateau, Grand Canyon, Arizona, consists of "western yellow pine, white fir, oak and New Mexican locust" with conditions "unusually dry" by the middle of June. I found the vegetation around Circleville and the Coral Pink Sand Dunes, both in Utah, characterized by junipers (*Juniperus* sp.), pinyon pine (*Pinus* sp.) and *Artemisia*, with groves of shrubby *Quercus* also found at the Dunes. The steep, south-facing slopes of Beaver Canyon, Utah, support junipers, *Cercocarpus*, and shrubby oaks, with a closed forest of ponderosa pine (*Pinus ponderosa*) and maple (*Acer* sp.) on the north-facing slopes. *Artemisia* and *Chrysothamnus* shrubs were scattered only on disturbed areas along roads in the canyon.

Habitats of this species range from 1714 to 2440 m in elevation.

Tipula (Eremotipula) leiocantha Alexander

Tipula (Lunatipula) leiocantha Alexander 1959: 132–134; Alexander 1965b: 37, cat.; Alexander 1967: 26, fig. 85 (male 9T, 1D, OD, 8S, Adm.), key, loc. (except records from San Diego and Ventura counties, which pertain to *diversa*); Theischinger & Theowald 1981: 25, cat.

Diagnosis.—*Male*: Hypopygium as in *diversa* group, including elongate OBL and prominent basistylar spine (as in Fig. 427); OBL nearly straight and almost flattened, with anterior ridge on lateral surface weakly developed (Fig. 387); ventral lobes of A9S with long, straight, slender, pale setae (Fig. 386). *Female*: Without brown, distinct thoracic stripes or pale patch extending along vein Cu and in *m* cells on wing; elongate pale inner ridges of 8S and overall whitish 8S; pigmentation stripes reduced or absent; hypogynial valves with rounded apex. Eastern California and western Nevada (Map 16).

Description.—*Length*: Male 17–20 mm ("15–16 mm", Alexander, 1959), female 22–24 mm. *Head*: Vertex and postgena yellowish brown to brownish-gray. Antennal length: male 4–5 mm, female 3 mm. *Thorax*: Overall yellowish brown to brown, pruinose. Males with presutural scutum with two pairs of parallel, longitudinal, brown to reddish brown stripes, stripes in females not strongly contrasting with reddish-brown background; area between inner stripes sometimes light reddish brown. *Legs*: Femoral rings brown, indistinct to distinct. Apices of tibiae slightly darkened. *Wing*: Male 16–17 mm ("15–16.5 mm", Alexander 1959) long, 4 mm wide; female 18–19 mm long, 4–5 mm wide. Overall light yellowish-brown; stigma brown, with small brown spot at end of Sc in males; wing slightly darker in females. Cell *sc* yellowish, cell *c* concolorous with rest of wing. Sometimes a faint darkening along margin of cell *a*₂. Pale areas proximal to stigma, at end of cell *r* and extending as band to cells *m*₃ and *m*₄. *Abdomen*: Terga 2–6 with sublateral, light brown to brown markings, usually proximally on each segment; line narrow and extending along entire length of terga 2; females with contiguous, pale lateral border. Median line along dorsum of abdomen

(Alexander 1959) usually faint or absent. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.5. Dorsal lobes subparallel, closely appressed to STP in dried specimens (Fig. 383), of moderate length, slightly longer than wide, broad at base, narrowing to subacute apex. Margins of lobes nearly smooth. STP elongate, ratio of length STP/9T = 0.5–0.7, compressed, with well-developed dorsal ridge along basal half. STP pale and abruptly narrowed in apical third, with dorsal margin deeply lacinate; cuticle at base faintly reticulate, relatively smooth distally. Ventral surface of shelf smooth or plicate. Ventral lobes mostly visible from above, convergent; each lobe broad (Fig. 384), smooth, usually with rounded apical margin and ventral ridge near base. *Ninth sternum* (+ *basistyle*): Lateral margin as in Fig. 427. Dorsomedial margin of BS straight opposite sp1. Dorsolateral margin of BS greatly produced opposite posterior condyle of ID, with thick, inwardly curved, short to elongate spine at apex (as in Fig. 427). Ventral lobes of A9S with long, pale, straight, slender, erect setae (Fig. 386). *Outer dististyle*: Posterodorsal margin straight, anterior extension long to short. *Inner dististyle*: Ventral surface of upper beak and apex of lower beak with well-developed ridges. Crest (Fig. 387) pale, low, roughly triangular, spinules throughout, dorsal margin straight and microscopically serrulate; without groove between crest and beak. OBL elongate, generally flattened and straight, L/W = 2.4–3.5, directed posteriorly and dorsal margin curled laterally 90° with respect to base of ID, of nearly uniform width beyond base of OBL, subapical region narrowed, sometimes abruptly, apex wide to narrow (Figs. 392–394, and subacute, but not greatly curved or twisted; a weakly developed, pale, longitudinal ridge laterally extending along basal third to half of lobe, setae in a row along ridge. *Adminiculum*: Lateral plates broadly expanded basally, emarginate dorsally with acute point just before or opposite dorsal spines (Fig. 390), each plate abruptly narrowed beyond point. Dorsal lobes fused at base, apices slightly separated and rounded, with parallel striae (Fig. 388). Median lobe small, about one-seventh to one-eighth total height of adminiculum, with lateral carinae extending from beak area. A pair of closely-set, dorsoventral ridges flanking posterior margin below median lobe (Fig. 389), each directed posteriorly, not laterally. *Eighth sternum*: Posterior (sclerotized) edge slightly concave.

Membranous apical region with broad band of long setae (Fig. 391), mostly 5–6 setae broad, wider laterally and at midlength. Setae carinate; setae about half as long as 8S. Behind setae, a pale, glabrous, flattened, membranous lobe (Fig. 391), slightly wider than long with rounded apical margin, a tiny sclerite sometimes on either side of membranous lobe, remaining area bare and tuberculate. *Ovipositor*: 8S elongate, outer cuticle mostly ivory to light yellowish brown, base brown; lateral edge with shallow to distinct cavity anteriorly (opposite inner ridge). Cerci extended, narrow (Fig. 410). Inner ridges of 8S elongate, as in Fig. 408, pale overall, with inner pigmentation stripes at most brown and granular in pattern (sometimes absent), outer stripes faintly indicated or absent. Vaginal apodeme broad subapically with edges roughened, an elongate attenuated tip dorsally.

Specimens examined.—*Type material*: Alexander (1959), in the original description of *leioanthra*, recorded the collection data of the holotype as "Big Pine Creek, Inyo County, California, on sage-covered hillside at Glacier Lodge, 7800 ft., July 11, 1957". Unfortunately, a pinned specimen marked as the holotype for this species and lacking a wing and the terminal half of the abdomen has completely different collection data: "California, Inyo Co., Bishop Creek, Intake camp, 8000' (2438 m), VII-8-57, C. P. Alexander". A microscope slide with a wing, two legs and male hypopygium, and marked as the holotype of *leioanthra*, is labeled with the Big Pine data given in the original description, along with "Holotype 10,403". The two ♂ paratypes, with parts on slides, are labeled as in the original description.

I think that it is possible to reconcile this difference in the collection data for the holotype of *leioanthra*. The apical margin of the base of the wing remaining on the pinned type specimen and the basal margin of the wing on the slide appear to match; also the pinned specimen lacks the abdomen beyond segment 4 and the abdomen on the slide lacks segments 1–4. Both of these observations provide a good indication that both the slide and pinned specimen marked "HOLOTYPE" make up the same individual. In addition, the Alexander collection has no slide marked "Bishop Creek, Intake camp" nor a pinned specimen lacking a slide of the abdomen and labeled "Big Pine Creek". The problem in establishing the correct type locality remains. Since

specimens are usually pinned and labeled far in advance of study and slide mounting, I think that it is more likely that the locality data on the pinned specimen is correct, and that the slide label of the holotype was confused with that of the paratypes at the time of mounting the wings and hypopygia of the three specimens. Therefore, I accept that the locality data on the pinned holotype is correct ("Bishop Creek, Intake camp", etc.), and that the type locality stated by Alexander (1959) is incorrect.

The holotype specimen is in good condition, those parts missing on the pinned specimen (wing, legs, hypopygium, antenna) being found on a microscope slide. The slide-mounted hypopygium is in fair condition, with the ninth sternum broken along the ventral midline, missing the membranous lobe between the eighth and ninth sterna and with both inner dististyles showing mesal views.

Other specimens: 26♂, 3♀. **USA: CALIFORNIA:** Inyo Co., Wyman Canyon, White Mountains, 9-VII-1967, at light, S. & S. Frommer, 1♂, 1♀ (UCR); 11 km N Parcher's Camp, 30-VI-1960, J. Buckett, 3♀ (ANSP, UCD); Mono Co., Coleville, (1573 m), 28-V-1939, M. Cazier, 1♂ (USNM); Lee Vining, (2067 m), 27-VI-1952, M.T. & H.B. James, 1♂ (WSU); Mono Lake, (1951 m), 27-VI-1949, Sperry, 1♂ (USNM); Tom's Place, 27-VII-1963, W. Chamberlain, 1♂, 1♀ (TAMU); Rock Creek Campground, 1 mi N of Tom's Place, 10-VIII-1963, C. A. Toschi, 1♂ (UCB); as preceding but 2195 m, 3-5-VII-1967, P. H. Arnaud, Jr., 7♂, 3♀ (CAS, JKG, UK); W Fork Walker River, Highway 108, Sonora Bridge campground, (2073 m), 26-VI-1980, Baumann & Stanger, 1♂, 1♀ (BYU); White Mountains, 3 mi N of Inyo Co., near Naval Research Station, N Fork of Crooked Creek, 10,150 ft (3094 m), 19-VIII-1963, flight trap, H. B. Leech, 1♂ (CAS); Crooked Creek, 3094m, 17-VII-1961, J. Drew, 2♀ (CAS); White Mountains, Mt. Barcroft, 3810 m, 16-VII-1961, J. Buckett, 1♀ (UCD). **NEVADA:** Douglas Co., Holbrook Junction, 14-VI-1957, P. L. and R. W. Coleman, 1♂ (CAS); Lander Co., Toiyabe Mountains, Kingston Creek, 5 km W Kingston, 2130m, 29-VI-1987, J. Rawlins, W. Zanol, 1♀ (CMNH); Kingston Camp, 30 mi S Austin, 7300 ft. (2225 m), 14-VII-1966, F. P. & M. Rindge, 2♂ (AMNH); Mineral Co., Telephone Canyon, Pilot Mountain, 1-VII-1952, Figg-Hoblyn, 3♂ (CAS); Washoe Co., Reno, (1369 m), 13-IV-1957, F. Parker, 1♂ (UCD).

Discussion.—Some variation was noted in the structure of the outer basal lobe of the inner dististyle, the ventral lobe of the ninth tergum, and the basistylar spine, but the variation does not seem to be correlated among these structures. In some specimens the outer basal lobe is broad and scarcely narrowing subapically (Fig. 394), while in others, e.g., the holotype, the lobe is narrow overall, and constricted subapically (Figs. 392, 393). The apex of the ventral lobe of the 9T is sometimes angulate and not evenly rounded (Fig. 385). The basistylar spine can be elongate and narrow, or short and wide.

Males of *leiocantha* are similar in most genitalic features to those of *evalynae* but can be most easily separated by comparing the lateral, longitudinal ridge on the outer basal lobe as detailed in the key. If the adminiculum is visible posteriorly, reference can be made to the ridges along its posterior margin. In *leiocantha*, these are strongly developed, while in *evalynae* they are absent. In addition, the subtergal process in *evalynae* is broad dorsoventrally, with a nearly truncate apex; in *leiocantha* it is narrower dorsoventrally, and the apical margin is subacute.

The females of *leiocantha* and *evalynae* are not clearly distinguishable, although the geographic ranges of the two species (based on male specimens) are narrowly separated by the western and central Great Basin in Nevada.

Relationships.—The species most closely related to *leiocantha* might be *evalynae*, based on the reduced size of the median lobe of the male adminiculum, and rugosity surrounding the membranous lobe between the male eighth and ninth sterna (latter character not used in the analyses; see end of character analysis section). Both of these features can be found as parallel derivations elsewhere within *Eremotipula*, although not among other species in the *diversa* species group. The dorsoventral ridges on the adminiculum, found in *leiocantha* and *lyrifera*, are arguably a synapomorphy of these two species, in conflict with the two features detailed above. Slight ridges in a similar location in *evalynae* appear to be homologous, but whether these are a reduction or the primitive condition cannot be ascertained. The shape and length of the outer basal lobe are similar in *leiocantha* and *evalynae*, but this might be symplesiomorphic.

Geographic distribution.—East central California (east side of the Sierra Nevada) and west

central Nevada (western edge of Great Basin) (Fig. 377).

Seasonal distribution.—April 13 to August 19. The great elevational range of *leioanthra* correlates with the long seasonal occurrence of adults of the species. Most adult records are from June and July.

Habitat.—Virtually nothing is known of the habitat of *Tipula leioanthra*. Alexander (1959) collected the paratype males "on sage-covered hill-sides" at Glacier Lodge, Mono Co., California. The range of the species in California closely approximates that of the sagebrush steppe along the eastern slope of the Sierra Nevada (Young, Evans & Major 1977: fig. 22-1).

The elevational range of this species is from 1369 m at Reno, Nevada, to 3094–3810 m in the White Mountains, California, with most records from 1950–2400 m. The elevations recorded in the White Mountains are the highest known for any species of *Eremotipula*. Mooney (1973) states that at about 3200 m in the White Mountains, limber pine (*Pinus flexilis*) and bristlecone pine (*P. longaeva*) are co-dominants, with understory vegetation including *Artemisia tridentata*.

Tipula (*Eremotipula*) *lyrifera* Dietz

Tipula lyrifera Dietz 1921: 5-6, fig. 2 (male hypo., dor.), key; Alexander 1948: 27, loc. (except records from Beaver and Mill Creek canyons which are *evalynae* and *diversa*); Alexander 1965b: 37, cat.; Theischinger & Theowald 1981: 27, cat.; Teale, 1984: 33, redesc., key, loc.

Tipula (*Lunatipula*) *carunculata* Alexander 1945a: 186-187; Alexander 1965a: fig. 9 (ID); Alexander 1965b: 35, cat.; Alexander 1967: 26, fig. 83 (male 9T without STP & VL; ID, 8S), key; Theischinger & Theowald 1981: 12, cat. **NEW SYNONYMY.**

Diagnosis.—*Male*: Hypopygium as in *diversa* group, including elongate outer basal lobe (Fig. 397); but distinguished by BS with two closely-set spines dorsolaterally, dorsal lobes of ninth tergum small, swollen, with strongly toothed apical margin (Fig. 395); ventral lobes of A9S with pale setae, only a few setae thickened. *Female*: Hypogynial valves short, about half length of cerci and strongly narrowed along posterior half; cerci broad, midlength width (viewed dorsally) only slightly less than that at base; 8S with inner ridges pale and elongate.

Description.—*Length*: Male 16–20 mm, female 18–28 mm. *Head*: Vertex and postgena yellowish brown to brown, heavily pruinose. Antennal length: male 5–6 mm, female 3–4 mm. *Thorax*: Overall yellowish brown to brown, and pruinose. Presutural scutum with two pairs of parallel, longitudinal, sometimes indistinct, reddish brown to dark brown stripes. *Legs*: Femoral rings scarcely evident in males, mostly distinct in females. *Wing*: Male 14–19 mm long, 4 mm wide. Female 16–22 mm long, 4–5 mm wide. Overall light brown, stigma brown; brown spot at end of Sc. Cells *c* and *sc* yellowed. Pale area nearly surrounding stigma, and extending as band along cord into discal, *m*₃ and *m*₄ cells. Pale along vein Cu and extending into cell *m* (most distinct in females). *Abdomen*: Terga 2–6 sometimes with a sublateral and dorsal brown spots in males. In females, a slender to broad, brown sublateral line along abdomen, with pale lateral bordering area, dorsal medial line sometimes present, mostly as a series of spots. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.4–0.5. Dorsal lobes subparallel, half as long as basal width, each swollen dorsomedially (Fig. 395), flattened and irregularly toothed along apical margin, sometimes finely dissected, teeth usually increasing in length laterally, and directed slightly ventrad. STP elongate, length of STP/9T = 0.6–0.7, dorsal ridge along entire length. STP equally wide and mostly sclerotized, abruptly narrowing and pale in apical fourth, dorsal margin strongly lacinate, apex sometimes bent slightly ventrad; cuticle near base with faint reticulations at 600x magnification. Ventral surface of shelf smooth. Ventral lobes mostly visible from above, slightly convergent (Fig. 396); each lobe smooth, broad basally, narrowing slightly to rounded apex. *Ninth sternum* (+ *basistyle*): Dorso-medial margin of BS relatively straight and smooth opposite sp1. Dorsolateral margin of BS with two closely-set spines opposite posterior condyle of ID; anterior spine small (rarely rounded; one specimen with spine undeveloped), posterior spine large and curved inward. Ventral lobes of A9S with many short, light colored setae, only 2–3 setae thickened and all slightly curved laterad. *Outer dististyle*: Posterodorsal margin nearly straight, anterior extension short to elongate (Fig. 399). *Inner dististyle*: Ventral surface of upper beak and dorsal surface of lower beak with weakly developed ridges. Crest pale (Fig. 397), low and usually subtriangular, dorsal margin

smooth. OBL elongate and flat, $L/W = 2.5\text{--}3.1$, wide in basal three fourths, particularly near midlength when viewed in a mesal aspect (Fig. 398), strongly narrowed in apical fourth, directed posteriorly and dorsal margin curled over 90° with respect to base of the OBL, a strong longitudinal ridge on lateral surface along dorsal margin, with row of setae. Apical portion digitiform, bent laterad but not twisted completely, apex rounded and without a notch. *Adminiculum*: Lateral plates broadly expanded throughout, emarginate dorsally with small lateral point beyond dorsal spines (Fig. 401), each plate abruptly narrowed beyond point. Dorsal lobes closely appressed basally, apices only slightly separated, rounded, with indistinct, parallel striae. Median lobe about one fourth height of total adminiculum, with elongate recurved beak (Fig. 400); posterior margin flanked by lateral carinae. Base below median lobe with a pair of closely set, dorsoventral ridges (Fig. 402) flanking margin, each directed posteriorly, not laterally. *Eighth sternum*: Posterior (sclerotized) edge shallowly concave. Membranous apical region with broad band of long setae, mostly 4–5 setae thick, wider at midlength, with setae near lobe shorter than remainder, but not in isolated group. Setae carinate, nearly equal in length to eighth sternum, extending to ventral lobe of A9S. Behind setae, a pale, glabrous, flattened, membranous lobe (Fig. 403), slightly longer than wide and usually with a small, pale, bare sclerite at each side (these sometimes absent); area otherwise bare and tuberculate. *Ovipositor*: Cerci broadened, particularly from midlength to near apex (Fig. 413) (scarcely wider at base than at midlength, cf. other species of species group with width at midlength about half that at base), lateral edge sometimes slightly irregular. 8S lateral edge with cavity anteriorly (opposite end of inner ridges). Inner ridges of 8S as in Fig. 409, elongate, pale overall, with pigmentation lines faintly evident only anteriorly, extending beyond the end of ridge. Hypogynial valves short, extending only half length of cerci, broad and dark at base, pale and strongly narrowed at midlength to apex. Vaginal apodeme (Figs. 360, 361).

Specimens examined.—*Type material*: *Tipula lyrifera* Dietz. Holotype ♂ (ANSP): UTAH: Utah Co., Vineyard, VI-6-1912, T. Spalding, Holotype #6394. The holotype of *lyrifera* is in only fair condition, but all necessary structures are present and visible, allowing confirmation of its identity. All

legs are broken off the specimen, except for two without tarsi; one leg is glued to a point under the specimen, along with the right antenna. The abdomen was broken at some previous time and glued to the thorax; the posterior apices of both inner dististyles are broken off.

Tipula carunculata Alexander. Holotype ♂ (USNM): NEVADA: Douglas Co., Kingsbury Grade, V-27-1939, M. Cazier, Holotype #7794. The right antenna, right front leg, right wing and abdomen beyond segment V of the pinned holotype of *carunculata* were removed from the pinned specimen by Alexander and mounted permanently on a similarly labeled microscope slide. On the slide, the posterior half of the ninth tergum is mounted ventral side up, with the ventral lobes broken. The membranous lobe is apparently missing from the eighth sternum. Other parts in good condition. Alexander (1967:26) emended the type locality information from California, Mono Co. (as stated in the original description and as written on the collection label), to Nevada, Douglas Co.

Other specimens: 103♂, 81♀. USA: CALIFORNIA: Alpine Co., Wolf Creek Road, ca. 11 km SE of Markleeville, ca. 1900 m, 4-VII-1969, P. H. Arnaud, Jr., 2♂ (CAS); Mono Co., Tom's Place, 27-VII-1963, W. Chamberlain, 1♀ (TAMU); as preceding but Rock Creek Campground, 2195 m, 3-5-VII-1967, P. H. Arnaud, Jr., 13♂, 5♀ (CAS, UK); Huntoon Camp, nr. Sonora Pass Junction, (1981 m, 6500 ft), 19-VII-1964, D. C. & K. A. Rentz, 1♂ (CAS); San Bernardino Co., San Bernardino Mountains, Barton Flat, 6250 ft (1905 m), 16-VII-1946, CPA, 1♂ (USNM); NEVADA: Washoe Co., Reno, VI-1911, R. W. Doane, 1♀ (CAS); Washoe Lake State Park, near Carson City, (4700 ft, 1433 m), 25-VI-1980, Baumann & Stanger, 1♂ (BYU); White Pine Co., 9.8 km E of McGill, along Timber Creek, 2430 m, 14-VI-1986, JKG #399, 16♂ (AMNH, CMNH, JKG, UK); Lehman Creek Campground, 11.3 km W Baker, 2286 m, 13-VI-1986, at light, JKG #395, M. F. Gelhaus, 1♂ (ANSP); Wheeler Peak vicinity, 12.9 km W, 2.4 km N of Baker, 2682 m, 12-13-VI-1986, JKG #396, 10♂ (JKG, UK, USNM). UTAH: Beaver Co., Mud Spring Ridge, 2.4 km E, 12.9 km N Manderfield, 2018 m, 11-VI-1986, JKG #393, 26♂, 33♀ (BYU, JKG, UK, USNM); Cache Co., Logan, (4535 ft, 1382 m), 24-VI-1938, at light, G. Knowlton, D. Hardy, G. Stains, 1♀ (USU); as preceding but 20-VI-1942, Knowlton, 1♂ (USNM); Blacksmith Fork Canyon, 14-16-VII-1964, Malaise trap, W. Hanson,

1 ♀ (USU); Iron Co., pass on Utah Highway #20, near Burnt Peak, 16.4 km E of US Highway # I-15, 2408 m, 10-VI-1986, JKG #390, 3 ♂, (JKG, UK); same as preceding but pupa coll. in soil under *Artemisia*, female emerged 18-VI-1986 (JKG); as preceding locality, 3-VIII-1964, H. Leech, 1 ♀ (CAS); Juab Co., Eureka, 11-16-VI-1920, 6-11-VI-1921, T. Spalding, 8 ♂ (ANSP); Millard Co., Fillmore, 31-V-1945, G. Knowlton, pinned specimen det. *lyrifera*, slide det. *carunculata*, both by CPA, 1 ♂ (USNM); Maple Grove Campground, Pavant Range, 13 mi E of Fillmore, 6600 ft (2012 m), 13-VI-1976, GWB #3, CWY, 3 ♂ (UK); Oak Creek, 3.3 mi E of Oak City, 5600 ft (1707 m), 12-VI-1976, GWB #1, CWY, 2 ♂ (KU); Piute Co., Pole Canyon, 16.1 km E, 4.8 km N of Junction, 2134 m, 9-VI-1986, JKG #388, 3 ♂ (JKG, UK); Tushar Mountains, City Creek Campground, 10.2 km NW Junction, 2320 m, 30-VI-1991, JKG #528, 3 ♂ (ANSP); Salt Lake Co., Salt Lake City, (4365 ft, 1330 m), 23-VI-1935, 1 ♂ (UMAA); Sanpete Co., Maple Canyon, 12-VI-1943, Knowlton & Telford, 1 ♂ (USNM); Tooele Co., Stansbury Mountains, Johnson Pass, (6237 ft, 1901 m), 11-VI-1955, at light, H. E. Cott, 1 ♂ (CAS); Utah Co., North Fork Provo Canyon, D. E. Hardy, 2? (BYU); Spanish Fork, 11-VI-1986, D. E. Hardy, 1 ♂ (USNM); Washington Co., Grass Valley, S. Pinto, 6800 ft (2073 m), 18-VI-1950, R. Miller & party, 1 ♀ (UMAA); Leeds Canyon, Oak Grove, 14-VI-1978, G. Knowlton, 1 ♂ (USU). WYOMING: Carbon Co., 2.1 mi NW Arlington, 19-VII-1981, R. Lavigne, 1? (probably ♂, abdomen destroyed in shipment, det. *lyrifera* by SAT, 1982) (UWL).

Discussion.—Alexander (1945a) compared *carunculata* briefly with *lyrifera*, stating only that the outer basal lobe in *carunculata* was "not twisted as in *lyrifera*". Alexander's concept of *lyrifera* was probably based on Dietz's erroneous illustration of the species, in which Dietz drew the outer basal lobe as strongly twisted or curled twice along its length, closer to the condition found in *diversa*. In fact, in *lyrifera* (including the type specimen), the outer basal lobe is relatively flat and straight, with only the apical region curved or bent laterad. Both Dietz (1921) and Alexander (1945) neglected to mention the double spines of the basistyle, and Dietz did not adequately describe or illustrate the strongly toothed dorsal lobes of the ninth tergum.

The holotype of *carunculata* exhibits several features unique to *lyrifera*: the dorsolateral margin of the basistyle shows two closely-set projections

(the larger one spine-like), and the dorsal lobes of the ninth tergum are small and swollen, with the apical margin strongly toothed (Alexander 1967: fig. 83). The smaller projection on the basistyle is more rounded than acute, but this is normal variation for *lyrifera*. I have seen individuals with a short spine on one side and the same structure rounded on the opposite side. All other details of the male hypopygium of *carunculata* agree as well with *lyrifera*. Therefore I propose the synonymy of the two names.

In the same year that Alexander described *carunculata*, he was determining specimens of the same species from Utah as *lyrifera* (based on specimen data; see also Alexander 1948). At some point, probably between 1965 and 1967, he considered *carunculata* to occur in Utah in addition to Nevada and changed at least one previous determination of *lyrifera* to *carunculata*. In addition, several other specimens that he determined as *lyrifera* are in fact *evalynae* or *diversa*.

Males and females of *lyrifera* are distinctive and not likely to be confused with those of other species. Males of no other species of *Eremotipula* have such swollen and strongly toothed dorsal lobes of the ninth tergum or double spines on the dorsolateral margin of the basistyle (the smaller spine is rounded in some individuals, but is usually at least produced). The shape of the outer basal lobe, particularly the generally straight, flattened blade with a laterally curved apical region, is also diagnostic.

The female hypogynial valve has a unique form and is shortened relative to most other species of *Eremotipula*. As in the distantly related species of the *eurystyla* group, which have reduced hypogynial valves and laterally broadened cerci, the cerci of *lyrifera* are also somewhat broadened, particularly in relation to other species in the *diversa* group. As mentioned for the *eurystyla* group, the broadened cerci and reduced hypogynial valve may represent adaptations to deep-boring oviposition (Hemmingsen 1956).

Relationships.—*Tipula lyrifera* is the sister species to *sackeni* + *diversa* (see discussion of phylogenetic analysis).

Geographic distribution.—South central Wyoming and central Utah, southwestward to east central and southeastern California (Fig. 414).

Seasonal distribution.—The emergence period for *lyrifera* is from late May to early August, with most records in June.

Habitat.—Information on habitats of *lyrifera* is available for eight localities in Nevada and Utah (JKG, GWB, field notes). At several localities in central Utah, e.g., Pole Canyon, I found *lyrifera* adults in vegetation dominated by *Artemisia tridentata*, *Pinus edulis* and *Juniperus* sp., with adults resting in the pine and juniper trees. Near Oak City, Utah, adults of *lyrifera* were found among the shrubby *Quercus* sp. bordering patches of *Chrysothamnus* and *Artemisia* shrubs, while in Maple Canyon, Utah, adults were found in a deciduous forest of *Acer* sp. and *Populus* sp., with undergrowth of *Rosa* and *Mahonia* (GWB, field notes).

I found *Tipula lyrifera* common at several sites in Nevada. Along Timber Creek, adults were abundant in sheltered herbage, with the surrounding area an open basin with *Artemisia tridentata* and *Purshia tridentata* (antelope brush). In the vicinity of Wheeler Peak, at the highest elevation known for this species (2682 m), adults were collected on a windswept slope amid stunted *Artemisia* shrubs, *Pinus monophylla* and tree-sized *Cercocarpus ledifolius*.

The elevational range of this species is from 1400 to 2700 m (4500–8850 ft), with the lowest habitats occurring in northern Utah and western Nevada, and the highest in the mountains of eastern Nevada and central Utah.

A single female of *lyrifera* was reared from a pupa collected in soil 7 cm deep under an *Artemisia tridentata* bush on a mountain pass in Iron Co., Utah. Pupal skins, undoubtedly of this species, were found also under *Artemisia* on a hillside in Pole Canyon, Utah.

Tipula (Eremotipula) sackeni, new species

*Tipula divers*a: Alexander 1945a: 412, loc., biol.

Diagnosis.—Wing with broad pale spot extending from cell *m* to *cu* and pale streak at base of cell *a*₁; dark spots at end of *Sc* and usually at origin of *Rs*, stigma dark. *Male*: hypopygium as in the *diversa* group, including elongate outer basal lobe and prominent basistylar spine (as in Fig. 427); OBL narrowed and bent apically (Fig. 6), with anterior ridge prominent (Fig. 4), and posterior margin (dorsad of posterior condyle) strongly convex; ventral lobes of A9S with numerous thickened, short, reddish brown setae. *Female*: 8S with mostly pale inner ridges and narrow lateral groove (Fig. 405).

Description.—*Length*: Male 16–20 mm, female 21–27 mm. *Head*: Male vertex and postgena yellowish brown to brown, females brown; pruinose. Antennal length: male 5 mm; female 3 mm. *Thorax*: Males overall yellowish brown to brown, females brown; pruinose. Males with presutural scutum with two pairs of distinct, longitudinal, light brown to brown stripes, stripes sometimes interrupted near midlength; stripes in females reddish brown to dark brown, contrasting with pruinose background, postsutural markings brown and distinct, scutellum with longitudinal line dark. Remainder of notum brown and pruinose. *Legs*: Femoral rings brown and distinct; tibial apices slightly darkened. *Wing*: Male 13–18 mm long, 3–4 mm wide; female 17–22 mm long, 4–5 mm wide. Overall light brown; stigma brown, with additional spot at end of *Sc* and sometimes at origin of *Rs*, also brown seam along *m-cu* and surrounding *Cu* vein and cell *m*. Pale area nearly surrounding stigma, extending as band along cord to cells *m*₃ and *m*₄, with single pale spot across cells *m*, *cu* and *a*₁ near midlength of wing; in females a pale streak at base of cell *A*₁. *Abdomen*: Terga usually unmarked dorsally. Terga 2–6 with dark brown, sublateral patches, pattern indistinct to nearly absent in some males, in females patches broadly contiguous, contrasting with pale lateral border; remainder of terga bright yellowish brown. *Hypopygium*: *Ninth tergum*: Ratio of length 9T/BS = 0.4–0.5. Dorsal lobes (Fig. 415) subparallel, of moderate length, slightly shorter than wide, broad basally, apex acute to nearly diagonally truncate; border slightly roughened. STP elongate, ratio of length STP/9T = 0.6–0.8, compressed, dorsal ridge indistinct, abruptly narrowing in apical third. Dorsum of STP lightly sclerotized in basal two thirds, remainder pale with margin strongly laciniate; cuticle of STP at base faintly reticulate. Cuticle of ventral shelf reticulate near margin. Ventral lobes partially visible from above, strongly convergent (Fig. 416); each lobe broad, smooth and rounded, with transverse ridge ventrally near apex. *Ninth sternum* (+ *basistyle*): Lateral margin as in Fig. 427. Dorsomedial margin of BS relatively straight. Dorsolateral margin of BS with inwardly-directed, elongate spine opposite posterior condyle of ID. Ventral lobes of A9S with dense, thickened, short, reddish-brown setae, setae curved strongly laterad. *Outer dististyle*: Posterodorsal margin straight, anterior extension moderate to long (Figs 424, 425).

Inner dististyle: Ventral surface of upper beak with well-developed ridges, those of lower beak indistinct. Crest (Figs. 4, 5) pale, low and broad, dorsal margin straight and microscopically serrulate; without groove between crest and beak. A large membranous area between crest and OBL. OBL elongate, sinuous, $L/W = 2.6-3.8$, directed posteriorly and dorsal margin curled laterally 90° with respect to base of lobe (Figs. 4, 6); longitudinal ridge well-developed anterodorsally, with single row of setae; OBL slightly expanded subapically beyond ridge, then narrowed to apex; apex partially twisted, usually digitiform (Fig. 5), but sometimes wide and rounded (Fig. 417). Posterior margin of ID strongly convex dorsad of posterior condyle (Fig. 5). *Adminiculum*: Lateral plates expanded basally, abruptly narrowed beyond dorsal spine (Fig. 420) with margin rounded. Dorsal lobes narrow, fused basally, apices separated, rounded, with parallel striae (Fig. 418). Median lobe large, lateral carinae flanking posterior margin, beak indistinct; dorsoventral ridges extending along each side of adminiculum. *Eighth sternum*: Posterior (sclerotized) edge shallowly concave (Fig. 421). Membranous apical region with a broad band (mostly 3–6 setae wide) of yellow setae, wider laterally and at midlength; two small patches of short to very short setae isolated from setal band and located in front of membranous lobe (Fig. 422). Setae in band carinate. Behind setal band, membranous lobe pale, glabrous, flattened and broad, slightly wider than long, with rounded apex (Fig. 422); a sclerotized area on either side of lobe, each sclerite extending onto lobe itself (Fig. 423), area otherwise bare. *Ovipositor*: 8S elongate, brown basally, with reddish brown medial line, remainder yellowish to cream. Inner ridges of 8S of moderate length, pale posteriorly, with pale brown, pigmentation extending two thirds length (as in Fig. 407); inner pigmentation dark brown and extensive. Outer lateral edge of 8S with slender, slightly curved shallow depression (Fig. 405) best viewed in dry specimen.

Specimens examined.—*Type material*: Holotype ♂ (UMAA): **CANADA: BRITISH COLUMBIA**, Robson V-21-40, H. R. Foxlee. Holotype in good condition, lacking only the right rear leg beyond the trochanter. Paratypes: 55♂, 75♀. **CANADA: BRITISH COLUMBIA**: Fernie, 3-VII, 1♂ (UMAA); Keremeos, 13-VI and 2-VIII, 1923, C. B. D. Garrett, 2♂ (USNM); Johnstone Creek Provincial Park, 16-VIII-1975, W. Lange, 1♀ (UCD); Lytton, 28-VI-

1931, G. J. Spencer, 1♂ (UBC); Oliver, 5-V to 19-VI, 1923, C. B. D. Garrett, 6♂, 1♀ (JKG, UK, USNM); as preceding but 8-V-1924, P. Vroom, 1♂ (USNM); Robson, 13-V to 26-VI, 1937–1940, H. R. Foxlee, some taken at light, 13♂, 20♀ (ANSP,UMAA); Salmo, 20-VI-1954, H. R. Foxlee, 1♂ (UMAA); Swansea Mountain, E of Invermere, 9-VII-1940, E. G. Marples, 1♂ (UBC). **MEXICO: BAJA CALIFORNIA**: Norte Ridge, Sierra San Pedro Martir, 9000 ft (2741 m), 4-VII-1968, D. Patterson, 1♂ (CAS). **USA: CALIFORNIA**: Alpine Co., West Fork Carson River, Snowshoe Springs Campground, 6600 ft (2010 m), 20-VI-1971, P. H. & M. Arnaud, 1♂ (CAS); Fresno Co., Huntington Lake, 7000 ft (2134 m), 7-16-VII-1919, E. Van Duzee, 2♀ (CAS); Glenn Co., Plaskett Meadows, NW corner of county, 6000 ft (1829 m), 27-VII-1960, H. Leech, 1♀ (CAS); Lassen Co., Susanville, 11-VII, Newcomer, 1♂, 2♀ (CAS); 2 mi N Susanville, 2-VII-1967, L. Dunning, 1♀ (UCD); Los Angeles Co., Big Pines, 29-VI-1948, A. L. Melander, 1♂ (USNM); Madera Co., Willow Meadow, SW foot Madera Peak, 7550 ft (2301 m), 12-VIII-1971, H. Leech, 1♀ (CAS); Willow Creek, 5600 ft (1701 m), 17-VII-1951, W. Day, 1♂, 3♀ (USNM); Mariposa Co., Miami Ranger Station, 1200m, 29-VI-1946, H. Chandler, 1♀ (CAS); Modoc Co., Canby, 4000 ft (1219 m), 19-20-VII-1982, C. & A. v. Nidek, 1♀ (ZMUA); Horse Camp, 6 mi E Perez, 1-VII-1934, J. Hewell, 1♀ (CAS); Mono Co., Leavitt Meadows, 2470 m, 7-VIII-1964, H. B. Leech, 2♂ (CAS); as preceding but 23-VII-1966, P. H. Arnaud, Jr., 1♂ (CAS); Nevada Co., Sagehen Creek, nr. Hobart Mills, 25-VI-1966, R. M. Bohart, 1♂ (UCD); as preceding but 7-21-VII-1976, D. Poirier & R. Montgomery, 3♀ (UCD); Placer Co., Brimstone Creek, 2.9 mi NE Foresthill, 3400 ft (1036 m), 8-VI-1976, GWB #4, CWY, 1♂ (UK); Squaw Valley, 1910 m, 31-VII-1988, at light, V. Lee, 1♂ (CAS); Tahoe National Forest, 4 km S of Tahoe City, 1900 m, 24-26-VII-1982, T. W. Davies, 1♂, 17♀ (ANSP,CAS); Ward Creek, 6.4 km SW Tahoe City, 2073 m, 28-VII-1982, T. Davies, 1♀ (CAS); Truckee River, 6000 ft (1828 m), 30-VI-1947, CPA, 1♂ (USNM); Plumas Co., Keddies, 14-VI-1940, Cazier & Aitken, 1♂ (USNM); San Bernardino Co., Camp O-Onco, nr. Running Springs, 6300 ft (1918 m), 19-VI-1976, C. L. Hogue, 2♂, 1♀ (LACM); Mill Creek, San Bernardino Mts., 6000 ft (1828 m), 12-VII-1947, 7-9-VII-1949, 2-VII-1950, 14-VII-1951, at light, Timberlake, 1♂, 5♀ (UCR); Sierra Co., Cottonwood Creek Campground, SE of Sierraville, 1767 m, 12-VIII-1967, P. Arnaud, 1♀

(CAS); Siskiyou Co., Mt. Shasta, McBride, 5000 ft. (1524 m), 26-VI-1967, K. Fender, 1♂ (USNM); Shasta Springs, 18-VI-1920, C. Fox, 1♀ (CAS); McBride Springs, 3 mi NNE Mt. Shasta City, 4500 ft (1372 m), 3-VII-1963, C. MacNeill & V. Whitehead, 1♀ (CAS); Tuolumne Co., Lyons Reservoir, 2-VI-1963, P. Arnaud, 1♀ (CAS); Unknown county, Lake Tahoe, 19-VII-(1876), O. Sacken, 1♂, 1♀ (MCZ). NEVADA: Douglas Co., Zephyr Cove, Lake Tahoe, 2-4-VII-1961, J. Buckett & S. Bailey, 2♀ (UCD); Ormsby Co., 1 mi E of L. Tahoe, 6900 ft (2101 m), 10-VII-1950, CPA, 1♂ (USNM); Washoe Co., Incline Village, 2-VIII-1965, D. Nichols, 2♀ (BYU); Pyramid Lake, Sutcliffe Station, 12-VI-1924, E. Hall, 1♀ (USNM). OREGON: Grant Co., Malheur National Forest, Beech Creek Forest Camp, 4800 ft (1463 m), 8-VIII-1967, K. & N. Fender, 1♂ (USNM); Jackson Co., Prospect, 23-V-1921, H. G. Dyar, 1♂ (USNM); Lake Co., Lakeview, 17-VIII-1963, D. G. Gray, 1♂ (BYU). WASHINGTON: Yakima Co., Tampico, (646 m) 23-V-1926, M. Lane, 1♂ (USNM). WYOMING: Teton Co., Jenny Lake, Grand Tetons, 6780 ft (2065 m), 1-9-VII-1941, CPA, 1♂, 1♀ (USNM).

Etymology.—*Tipula sackeni* is named after C. R. Osten Sacken, not only in honor of his great achievements in dipterology, particularly regarding the systematics of the Tipulidae, but also for his having collected the first specimens of any species of *Eremotipula*, now paratypes of *Tipula sackeni*, at Lake Tahoe, California, in July 1876.

Discussion.—Besides variation in overall body coloration, some variation is seen in the structures of the male hypopygium of *Tipula sackeni*. The outer dististyle varies in the length of the anterior extension (Figs. 424, 425), and the apex of the outer basal lobe of the ID varies from broad to narrow, although it is usually narrow and digitiform. The most interesting variation is seen in the length of the setae found in small groups directly in front of the membranous lobe of the eighth sternum (Fig. 422). In several specimens from Nevada (Ormsby Co.) and California (Mono Co.), these setae are only about as long or slightly longer than the height of the lobe, but they are much longer in specimens from other parts of the range.

Tipula sackeni has been confused repeatedly with *diversa* (e.g., Alexander 1945: 412) in several museum collections, but several features as used in the key allow separation of the males of these two species, including the structure of the outer basal lobe of the inner dististyle. Other characters

separating the males of the two species are the lack of a spine on the lateral plates of the adminiculum in *sackeni* (present in *diversa*) and the slightly more elongate and setose band of setae on the apex of the eighth sternum in *sackeni*. Females can be distinguished from other members of the *diversa* group, particularly *diversa*, by the characters listed in the key and discussed under the *diversa* section. In addition the geographic distributions of these sister species are mostly allopatric.

Relationships.—*Tipula sackeni* is the sister species of *diversa*, based on several synapomorphies (see phylogenetic analyses). In light of this strong evidence, the lack of a spine on the margin of the lateral plate of the adminiculum must be considered as a loss in *sackeni* instead of a primitive absence. In fact, some specimens do exhibit a slight angulation of the margin opposite the dorsal spines, precisely where a spine might be expected.

Geographic distribution.—Southern British Columbia, Canada, to northern Baja California, Mexico; also northwestern Wyoming (Fig. 426).

Tipula sackeni occurs over a wider range of latitudes than any other species of *Eremotipula*. It is the only species that has been collected in Mexico. The fragmented distribution of this species is of particular interest. It is certainly due in part to a lack of collecting, but this is probably only part of the explanation. Other species of *Eremotipula* have been collected in areas where *Tipula sackeni* is not known to occur, e.g., eastern Washington, and therefore the lack of records there may indicate a real absence.

Seasonal distribution.—*Tipula sackeni* is in flight from May 5 to August 17, according to collection records from over the entire range of the species. At two sites where many specimens have been secured, Oliver and Robson, British Columbia, adults can be found for well over a month, from early May to the middle of June.

Habitat.—The habitats of *sackeni* are poorly known. Alexander (1945a, as *diversa*) found the species to be rare in the Teton Mountains of Wyoming, occurring in a forest of mostly lodgepole pine (*Pinus contorta*). Byers (field notes) collected a single male in Placer Co., California, from a slope forested by ponderosa pine (*P. ponderosa*), incense cedar (*Calocedrus decurrens*), alder (*Alnus* sp.) and Douglas-fir (*Pseudotsuga menziesii*).

This species inhabits a large elevational range, from over 2700 m (9000 ft) in the mountains of

Baja California, 1035–2470 m (3400–8100 ft) in the Sierra Nevada mountains of California, to lower elevations of 170–1000 m (565–3300 ft) in southern British Columbia.

Tipula (Eremotipula) diversa Dietz

Tipula diversa Dietz 1921: 4–5, fig. 1, 1a (male hypo., dor., lat.), key; Alexander 1945a: 412, misident. of *Tipula sackeni* n. sp.; Alexander 1946a: 506; Alexander 1948: 26, loc.; Alexander 1965b: 35, cat.; Theischinger & Theowald 1981: 17, cat.; Teale 1984: 30–31, redesc., loc., key, biol.

Tipula leiocantha: Alexander 1967: 26 (specimens from San Diego and Ventura counties).

Tipula lyrifera: Alexander 1948: 27 (specimen from Mill Creek, Salt Lake Co., Utah).

Diagnosis.—Wing with large pale patch extending from cell *m* to *A*₁, pale streak at base of cell *a*₁; dark spots at end of *Sc* and origin of *Rs*, stigma dark (see Frontispiece, Fig. 456). *Male*: Hypopygium similar to others in *diversa* group, including elongate outer basal lobe and prominent basistylar spine (Fig. 427), OBL with posterior margin (dorsad of posterior condyle) strongly convex, anterior ridge obsolete, and apex twisted (Fig. 431) and ventral lobes of *A9S* with numerous, thickened, short, reddish brown setae (Fig. 430). *Female*: 8*S* with elongate, pale inner ridges (Fig. 407), lateral edge with straight broad groove (Fig. 406).

Description.—*Length*: Male 18–22 mm, female 21–29 mm. *Head*: Male vertex and postgena yellowish brown to brownish gray, pruinose; female brownish gray. Antennal length: male 4–6 mm; female 3–4 mm. *Thorax*: Overall brown, pruinose. Presutural scutum with two pairs of parallel, longitudinal, yellowish brown to brown stripes in male; in female, stripes brown to dark brown, contrasting from background, other markings on postscutum distinct, a dark longitudinal line on scutellum. *Legs*: Femoral rings brown to dark brown, distinct. *Wing*: Male 14–20 mm long, 4–5 mm wide; female 17–22 mm long, 4–6 mm wide; overall light brown; stigma brown, with additional brown spots at end of *Sc* and sometimes at origin of *Rs*; brown seaming along *m-cu* (particularly females) and surrounding vein *Cu* to wing margin (Fig. 456). Pale area nearly surrounding stigma, and extending as band along cord into discal, *m*₃ and *m*₄ cells, large pale patch in cell *m* at midlength contiguous with pale streak along *A*₁;

an additional streak in cell *a*₁. *Abdomen*: In males, dark patches dorsomedially and sublateral on terga 2–5 but not forming continuous lines. In females, sublateral dark patches broad and continuous or nearly so, bordered laterally by pale tergal border; segments bordered posteriorly also by thin pale line. Remainder of female terga bright yellowish brown, usually with thin medial brown line (not continuous with other segments). *Hypopygium*: *Ninth tergum*: Ratio of length 9*T*/*BS* = 0.4–0.5. Dorsal lobes subparallel, of moderate length, width equal to length or slightly wider, broad at base, narrowing to acute apex (Fig. 428); borders slightly irregular. STP elongate, ratio of length STP/9*T* = 0.7–0.8, compressed, with dorsal ridge extending entire length, narrowing slightly at apex. Process slightly sclerotized in basal half (mostly dorsal), remainder pale with margin deeply laciniate; cuticle at base weakly reticulate. Ventral surface of shelf smooth. Ventral lobes mostly visible from above, strongly convergent (Fig. 429); each broad, smooth, with rounded apical margin and transverse line near apex, sometimes forming a strong ridge ventrally. *Ninth sternum* (+ *basistyle*): Lateral margin as in Fig. 427. Dorsomedial margin of *BS* relatively straight opposite *sp*₁. Dorsolateral margin of *BS* greatly produced opposite posterior condyle of *ID*, an elongate, inwardly-directed spine at apex. Ventral lobes of *A9S* with dense, thickened, reddish brown, short setae (Fig. 430), setae directed laterad. *Outer dististyle*: Posterodorsal margin nearly straight, anterior extension extremely long (Fig. 427). *Inner dististyle*: Ventral surface of upper beak and dorsal surface of lower beak with ridges. Crest (Fig. 431) pale, low and broad, subtriangular, dorsal margin appearing entire but microscopically serrulate; without groove between crest and beak. A large membranous area between crest and OBL. OBL elongate, nearly straight, *L/W* = 2.8–3.6, directed posteriorly with dorsal margin curled laterally 90% with respect to base of *ID*, lobe narrowing gradually to apex; a slight longitudinal ridge anteriorly with a row of setae. Apex of OBL twisted, apical margin rounded, usually with slight notch. Posterior margin of *ID* dorsad of posterior condyle broadly convex. *Adminiculum*: Lateral plates expanded throughout, emarginate dorsally with small lateral point opposite dorsal spine (Fig. 433), each plate abruptly narrowed beyond point. Dorsal lobes fused basally, apices slightly separated and rounded, with

mostly parallel striae. Median lobe large (Fig. 432), height about half that of total adminiculum; a pair of carinae flanking posterior margin (Fig. 434); ventral margin roughened, a prominent vertical ridge on either side of lobe. *Eighth sternum*: Posterior (sclerotized) edge shallowly concave. Membranous apical region with broad band of long setae, mostly 2–3 setae thick, wider laterally and at midlength; two small patches of shorter setae isolated from setal band and located in front of membranous lobe. Setae carinate. Behind setae, a pale, glabrous, flattened, median, membranous lobe, about 1.5x as wide as long, remaining area glabrous. *Ovipositor*: 8S elongate, with base of hypogynial valves beyond base of cerci; dark at base with median line, remainder cream to yellowish white. Cerci elongate, narrow (Fig. 411). Each inner ridge of 8S elongate, 1.3–1.5 mm long, pale yellowish, with faint brown pigmentation extending along outer surface (Fig. 407), inner pigmentation darker and more extensive. Outer lateral edge of 8S with broad, elongate, mostly straight, groove (Fig. 406), most visible in dried specimens.

Specimens examined.—*Type material*: Holotype ♂ (ANSP): UTAH: Utah Co., Vineyard, VI-1-1912, T. Spalding, Holotype #6395. The holotype is in good condition but lacks three legs, with the remaining legs glued to the body. There is a small tear in the costal region of the left wing. Allotype ♀, NEW MEXICO: Grant Co., Silver City, VI-2-1913. Paratypes: 4♂, 1♀, 2 sex?; locality data as for allotype except dates are V-25 to VI-10-1913, and V-29-19, (2♂ USNM, others ANSP); COLORADO: Gilpin Co., Clear Creek, VI-23-1914, 1♂, (ANSP); COLORADO: Jefferson Co., Platte Canyon, VI-27-1915, 1♂ (ANSP).

Other specimens: 158♂, 86♀. ARIZONA: Coconino Co., 7 mi E Jacob Lake, 6800 ft (2073 m), 21-VII-1965, F. P. & M. Rindge, 3♀ (AMNH); Double Springs camp, west side of Lake Mormon, 7140 ft (2176 m), 11-VI-1979, GWB #5, 1♂ (UK); Grand Canyon, Kaibab Plateau, 8000 ft (2438 m), 17-18-VI-1942, CPA, 8♂, 4♀, 1? (USNM); Oak Creek Canyon, 13-17-VI-1941, Sperry, 6♂ (USNM); as preceding, 5-VI-1949, N. Cricknar, 1♀ (USNM); as preceding but 5500 ft (5180 m), 10-12-VI-1942, CPA, 6♂, 7♀, 2? (USNM); as preceding but Bootlegger Camp area, 5300 ft (1615m), 11-VI-1979, GWB #3, 1♂ (UK); Williams, 2-VII-1953, E. S. Ross, 1♂ (CAS); Gila Co., Christopher Creek, Mogollon Rim, 5800 ft (1768 m), 17-VI-1957, L. M. Martin et al., 1♂, 1♀,

1? (LACM); Parker Creek, Sierra Ancha, 2-7-V-1947, H. & M. Townes, 2♂ (UMAA); White Mts., 6000 ft (1829 m), 26-VI-1925, O. C. Poling, 3♂, 2♀ (UMAA); Gila-Pinal counties, Miami, Pinal Mts., 5000 ft (1524 m), 18-22-V-1925, O. C. Poling, 4♂, 1♀ (UMAA); Greenlee Co., White Mountains, Granville Campground, 2100m, 28-V-1993, JKG #600, C. Nelson, D. Koenig, 2♀ (ANSP); Maricopa Co., Avondale, 10-IV-1927, O. C. Poling, 1♂, 2♀ (UMAA); Mohave Co., Hualapai Mountain Park, 9.5 mi ESE of Kingman, 4800 ft (1463 m), 26-V-1979, GWB #2, JKG, 5♂, 2♀ (UK); as preceding but Wheeler Spring and Pine Knoll campground, 8-VI-1982, Baumann and Clark, 13♂, 3♀ (BYU); Navaho Co., Highway #77, 6.5 mi S of Snowflake, 6500 ft (1981 m), 24-V-1979, GWB #1, K. Spillman, 1♂ (UK); Yavapai Co., Ash Creek ENE Dewey, 30-31-V-1950, R. R. Miller & party, 1♀ (UMAA); 4 mi N Granite Dells, Prescott, 11-VI-1970, L. M. Martin, 1♀ (LACM); Oak Creek Canyon, 25-V-1950, R. R. Miller & party, 1♀ (UMAA); Yarnell, Weaver Mts., 24-V and 10-VI, 1937, L. K. Gloyd, 2♂, 1♀ (USNM). CALIFORNIA: Riverside Co., Idyllwild, San Jacinto Mts., 10-VI-1939, J. G. Shanafelt, 1♂ (LACM); San Bernardino Co., Camp O'Ongo, nr. Running Springs, 6200 ft (1890 m), 19-VI-1976, C. L. and J. N. Hogue, 1♂, 1♀ (LACM); San Diego Co., Mt. Laguna, 21-VI-1963, J. Powell & others, det. *leiocantha* by CPA 1964, 2♂, 3♀ (UCB, UCD); Ventura Co., Ozena Forest Camp, 3200 ft (975 m), 18-VI-1963, Kirkwood, det. *leiocantha* by CPA, 1♂ (USNM). COLORADO: Archuleta Co., Lower Piedra Campground, Piedra River, 28-VII-1980, Baumann & Cox, 1♂ (BYU); Garfield Co., Glenwood Springs, 27-VI-1918, Oslar, 1♂ (UMAA); Montezuma Co., 12.2 km E of Cortez on Co. Rd. #34, ca. 1981 m, 6-VI-1986, JKG #379, 1♂, 2♀ (JKG). NEVADA: Clark Co., Lee Canyon, 24-V-1940, Cazier et al., 1♂ (USNM). NEW MEXICO: Bernalillo Co., Sunset Canyon, Albuquerque, 1920 m, 23-V-1979, GWB & party, 1♀ (UK); as preceding but larvae coll. 9-IV-1983, adults emerged 6-7-V-1983, JKG Rearing #207, 1♂, 1♀ (JKG); Embudo Canyon Trailhead, Albuquerque, 1768 m, 25-V-1991, JKG #501, C. Nelson, 4♂, 4♀ (ANSP); Doña Ana Co., Organ Mountains, Aguirre Springs Campground, 4.8 km E Organ, 1707 m, 10-IV-1986, JKG #324, 1♀ (ANSP); as preceding but 30-V-1991, at UV light, JKG #513, C. Nelson, 3♀ (ANSP); Grant Co., Silver City, V-25 & VI-13, 1913, 2♀ (ANSP); Lincoln Co., Jicarilla Mountains, near Jicarilla, 27-V-1991, at light, JKG

#508, C. Nelson, 1♂ (ANSP); Otero Co., White Mts., 7000 ft (2134 m), 20-VII-1927, O. C. Poling, 1♂, 2♀ (UMAA); Sandoval Co., Frijoles Canyon, 18-VI-1942, Sperry, 1♂ (USNM); Sandia Mts., 5.3 mi SSE of Placitas, 6500 ft (1981 m), 15-VI-1979, GWB #5, 2♂ (UK); Socorro Co., Bear Trap Camp, 28 mi SW Magdalena, 8500 ft (2591 m), 5-VII-1965, F. P. & M. Rindge, 1♀ (AMNH); Taos Co., Red River Canyon, 11.5 mi E of Questa, 8600 ft (2621 m), 26-VI-1981, at light, SAT, 1♂ (UK). UTAH: Beaver Co., Beaver (High Lowe Creek and Pond, in mtns. above Beaver), 8000 ft (2438 m), 26-VI-1942, CPA, 1♂ (USNM); Beaver Canyon, 12-VII-1945, Knowlton, 1♂, 1♀ (USNM); Cache Co., Blacksmith Fork Canyon, 14-16-VII-1964, Malaise trap, W. J. Hanson, 3♂, 2♀ (USU); Green Canyon, 25-VII to 6 VIII-1964, Malaise trap, W. J. Hanson, 3♂ (USU); Logan Canyon, 24-VI-1956, G. Knowlton, 1♂ (UK); Logan Canyon, 4800 ft (1463 m), 30-VI-1942, CPA, 1♂ (USNM); as preceding but 8-VIII-1945, Knowlton, 1♂ (USNM); Kane Co., Glendale, Circle VH Ranch, 26-VI-1941, Sperry, 1♂, 1♀ (USNM); Millard Co., Oak Creek, 3.3 mi SE Oak City, 5600 ft (1707 m), 13-VI-1976, GWB #2, CWY, 22♂, 4♀ (UK); Piute Co., Birch Creek Canyon, 1.6 km S, 3.2 km W of Circleville, 1963 m, 10-VI-1986, JKG #389, 3♂, 3♀ (JKG); Salt Lake Co., Mill Creek Canyon, 4475 ft (1364 m), 24-VI-1938, Knowlton & Hardy, det. *lyrifera* by CPA 1948, 1♂ (USU); San Juan Co., Devils Canyon Campground, 18 km SW of Monticello on US Hwy. #191, 2164 m, 6-VI-1986, JKG #380, 7♂, 1♀ (CMNH, JKG, UK); Sanpete Co., Maple Canyon, 12-VI-1943, Knowlton & Telford, 1♂ (USNM); Tooele Co., Settlement Canyon, 5100 ft (1554 m), VI-1943, Knowlton, 1♂ (USNM); Stansbury Mountains, S Willow Canyon, 13-VIII-1953, stream side, H. Cott, 1♀ (BYU); Stockton, 2-VII-1914, T. Spalding, 3♀ (MCZ); Utah Co., Provo, V. M. Tanner, 2♂ (BYU); as preceding but H. Thomas, 1♂ (USNM); Provo, Rock Canyon, 27-VI-1984, C. R. Nelson, 2♂ (BYU); Spanish Fork, 19-V to 10-VI, 1936, D. E. Hardy, 6♂, 1♀, 1? (USNM, USU); Springville foothills, 30-VII-1986, C. Nelson, N. Penny, 1♀ (ANSP); Timpanogos Cave National Monument, 4 mi E Alpine, 15-VI-1964, D. Huntzinger, 1♀ (BYU); Washington Co., 6.9 km W of Central, 1859 m, larvae coll. 30-IV-1986, in soil under *Cowania mexicana*, adults emerged 18-24-V-1986, JKG #365, Rearing #291-D, 3♂, 6♀ (JKG); Leeds Canyon, 26-V-1974, Hanson

& Knowlton, 3♂, 2♀ (USU); as preceding but Oak Grove Camp, 5-VI-1964, at light, W. J. Hanson, 1♂ (USU); as preceding but 14-VI-1978, G. Knowlton, 1♂, 1♀ (USU); Little Pine Creek below Enterprise Reservoir, 3-VI-1983, M. Whiting, 1♂ (BYU); North Juniper Campground, Santa Clara River, 6-VI-1981, R. W. Baumann, 1♂ (BYU); Pine Valley Campground, 16-VII-1980, Hanson & party, 1♂ (USU); Zion National Park, 4500 ft (1372 m), 21-22-VI-1942, CPA, 3♂, 1? (USNM); as preceding but 24-VI-1949, W. Lange, 1♀ (UCD); no further data, Osten Sacken, 1♂, (MCZ). WYOMING: Carbon Co., Bottle Creek Camp, 7 mi SW Encampment, 8800 ft (2682 m), 2-VIII-1967, F., P. & M. Rindge, 1♂, 6♀ (AMNH).

Discussion.—The date on the allotype label differs from that stated by Dietz (V-24-1913 vs. VI-2-1913), but none of his female specimens bears the date he mentions. Two males from Silver City, although clearly labeled paratypes, were not listed in his original paper. All paratype males are conspecific with the holotype.

Illustrations of the male hypopygium of *diversa* that accompany Dietz's original description are highly diagrammatic and inaccurate, particularly regarding the inner and outer dististyles.

Alexander (1967) confused *diversa* with *leiocantha*, probably due to the fact that these are the only two species in the *diversa* group which lack the well developed ridge on the outer basal lobe. Several other features of the outer basal lobe can be used to distinguish easily between males of the two species. In *diversa*, the posterior margin dorsal of the posterior condyle is strongly convex, and the blade of the OBL is longer, strongly tapered, with a twisted apex. In *leiocantha*, the basal margin is slightly concave, and the blade is shorter, not strongly tapered, and with a straight apex.

Females of *diversa* are difficult to distinguish from other species in this species group. The thoracic and wing patterning will distinguish this species from *evalyinae* and *leiocantha* and the development of the groove on the 8S distinguishes *diversa* females from those of *sackenii*. In addition, these latter two species only slightly overlap in geographic distribution (Transverse Ranges of California).

Relationships.—The close relationship of *Tipula diversa* and *T. sackenii* is evidenced by several synapomorphies, as detailed in the phylogenetic

analyses. The reduction of the longitudinal ridge on the outer basal lobe of the inner dististyle in *diversa* and *leiocantha* must be interpreted as a parallelism, as this feature conflicts with several, equally convincing characters placing *diversa* close to *sackenii*.

Geographic distribution.—South central Wyoming, Colorado and northern Utah southward to southern New Mexico and Arizona, westward to southern Nevada and southern California (Fig. 435).

Seasonal distribution.—Correlated with its widespread distribution, *Tipula diversa* has a long adult emergence period over its entire range, from April 10 to August 13. Earliest adult records are for lower elevations in Arizona, New Mexico and Utah, with the latest seasonal records, in July and August, for high elevations in Colorado, New Mexico, Utah and Wyoming. Most collections were made in May and June.

Habitat.—*Tipula diversa* has been collected most often in Great Basin conifer woodland (Brown 1982a), with pinyon pine and juniper abundant, and including an understory of shrubs such as *Artemisia tridentata*, *Cercocarpus* sp., *Cowania mexicana*, and *Chrysothamnus* spp. (Byers, Gelhaus, field notes). At higher elevations, e.g., in Carbon Co., Wyoming, *diversa* is found in habitat with a mixture of sagebrush and forests of fir, spruce, oak or ponderosa pine (Gelhaus, field notes; also see Alexander 1946a, 1948). In southern New Mexico, at Aguirre Springs, vegetation was dominated by live oak and juniper, apache plume, *Rhus trilobata*, and other shrubs (Gelhaus, field notes). I have little information regarding the habitats of *diversa* in southern Arizona and California.

Tipula diversa can be found at 975 m (3200 ft) in Ventura Co., California, to 2682 m (8800 ft) in Carbon Co., Wyoming. Most collections occurred between 1500 and 2000 m.

I have reared this species twice, from sites in Washington Co., Utah, and Bernalillo Co., New Mexico. Larvae were found at both localities in the soil under a thin layer of detritus primarily under shrubs of *Cowania*, but other shrubs were intermixed with the *Cowania* (including *Artemisia* and *Chrysothamnus*) at the Utah site. Further details regarding the rearing from New Mexico can be consulted in the "Habitat" section of *anasazi*. In both instances, *diversa* started emerging in the lab-

oratory at the end of the emergence period for the other species of *Eremotipula* present (*madina* and *kaibabensis* in Utah, *anasazi* in New Mexico). Larvae were nearly mature when collected in early April in New Mexico, and were mature when collected in late April in Utah.

HISTORICAL BIOGEOGRAPHY

Understanding the historical biogeography of western North America is complicated by many factors, including orogeny and severe climatic shifts (Minckley *et al.* 1986). Some authors such as Cracraft (1988), have expressed concerns that no current historical biogeographic methodology, such as vicariance or cladistic biogeography (Platnick & Nelson 1978; Nelson & Platnick 1981; Humphries & Parenti 1986) can retrieve the complex, often conflicting patterns of area relationships that arise during the long history of a continental biota, particularly due to the loss of integrity of endemic areas due to intermittent barriers and dispersion. Noonan (1988) evaluated this point by examining the empirical evidence, i.e., area relationships implied by the cladograms for 22 genera of North American insects. Although he identified ten general patterns of disjunctions for North America, only three reduced area cladograms were found to have congruent area relationships for three or more areas. Noonan cited the lack of congruence in the insect data to dispersal across barriers, drastic shifts in species ranges due to Pleistocene and Pliocene glaciations, cyclical appearance and disappearance of barriers, and extinctions. Other factors are that too few cladograms of insects exist for the entire continent, and a lack of concentration of any cladograms for any limited set of areas, such as the desert Southwest.

Tipula (Eremotipula) offers several strengths for such analyses for western North America (particularly arid and xeromontane areas), including a high diversity and endemism of species in the region, demonstration of the group's monophyly and an available hypothesis of the included species phylogenetic relationships. These strengths, though, must be tempered by the uncertainties that remain in the phylogenetic analyses and the incompletely known distributions of the species.

I have separated the biogeographic analysis of *Eremotipula* into four sections: (a) areas of endemism, (b) sister species vicariance, (c) relationship of desert areas, and (d) evolution of habitat use.

AREAS OF ENDEMISM

Few authors are explicit in their criteria for recognition of areas of endemism (e.g., Noonan 1988) and this concept is not clearly defined in even the most basic discussions of cladistic biogeographic methodology (e.g., Humphries & Parenti 1986). In this study, areas have been recognized as endemic areas when inhabited by one or more species or monophyletic groups whose range(s) does not exceed 1000 km in extent, and do not encompass more restrictive areas inhabited by other species. These criteria, although admittedly in part arbitrary, follow that used by previous western North American biogeographic studies, such as Kavanaugh (1980), and have allowed comparisons with those studies. These criteria also serve as a starting point for identifying areas represented by the species of *Tipula* (*Eremotipula*), with the validity of these areas tested by future studies of desert crane fly groups and other segments of the biota. Since many distributions most likely date from the late Pleistocene, correlation of areas with available habitat (as shown by paleobotanical evidence) is taken as further support. For example, several species of *Eremotipula* (*impudica*, *sinistra*) show congruent distributions encompassing the northern Great Basin and Rocky Mountains (to the Okanagan Valley, British Columbia) but the range exceeds the distance criteria and the area likely supported subalpine or tundra habitat during the Wisconsin, both characteristics not considered indicative of an area of endemism and more probably suggestive of dispersion or diffusion from southern refugia in the Holocene.

I have identified 12 areas of endemism in western North America, based on the above criteria and known distributions of *Eremotipula* species (areas #1–12, Fig. 436). The taxa inhabiting these areas are listed in Table 6. Several areas are particularly rich in species, e.g., area 1 (Mojave, 5 spp.) and areas surrounding and including the Great Basin, e.g., areas 3 and 4 (Sierra Nevada, 4 spp.), areas 5–7 (northern and eastern rims of the Great

Basin, 6 spp.) and areas 8–10 (Colorado Plateau, 6 species). Only two areas are noted in the northern Sonoran desert region of Arizona (areas 11–12, 3 spp.), and none in the Chihuahuan Desert. Additional support for these areas comes from ongoing studies of other desert crane fly groups in *Luuatipula* (Gelhaus, unpublished data). Some of these areas correspond with areas of endemism identified by Noonan (1990) for the carabid beetle genus *Harpalus*, and in addition, are inhabited by other endemic insects in diverse habitats, such as aquatic stoneflies (Nelson & Baumann 1987) mirid plant bugs (Stonedahl & Schwartz 1986; Stonedahl & Schuh 1986), aquatic beetles (Perkins 1980), weevils (Anderson 1988) and moths (Lafontaine 1982). These taxa corroborating the areas of endemism are listed in Table 6.

SISTER SPECIES VICARIANCE

The subgenus *Eremotipula* has seven pairs of allopatric species pairs (Table 7) with two other pairs possible depending on interpretation of character data (marked in Table 7 with an asterisk). None of these area disjunctions are replicated within these groups and only two correspond with the ten North American disjunction zones designated by Noonan (1988); *incisa*-rest of *Eremotipula* corresponds to Zone 1a, eastern and western North America; and *diversa-sackeni* corresponds to Zone 5, Mogollon Rim/SE Colorado Plateau. As crane flies appear to have moderate vagility (Tangelder 1988) and some species of *Eremotipula* have apparently moved over 1000 km north to southern British Columbia since the last glaciation (e.g., *impudica*, *sinistra*, *sackeni*), it seems likely that many of these allopatric distributions also date from the last glacial period, or about 9,000–14,000 years ago (Kavanaugh 1979, Lafontaine 1982). At a broader level (species groups) some allopatric disjunctions are replicated although the exact endemic areas may differ: disjunction across the Great Basin (2 pairs), disjunction between the Great Basin and Mojave (2 pairs) and disjunction between the Mogollon Rim and either the Great Basin or northern Colorado Plateau (3 pairs).

RELATIONSHIP OF DESERT AREAS

The subgenus *Eremotipula* corresponds with the North American Desert and Plains Track of

Table 6. Areas of endemism in western North America for *Tipula* (*Eremotipula*) and some *Tipula* (*Lunatipula*).

No.	Area	<i>Tipula</i> spp. endemics	Other insect endemics
1	Mohave (Transverse Ranges)	(<i>E.</i>) <i>biproducia</i> (<i>E.</i>) <i>larreae</i> n. sp. (<i>E.</i>) <i>melanderiana</i> (<i>E.</i>) <i>schusteri</i> (<i>E.</i>) <i>spinosa</i> n. sp. (<i>L.</i>) <i>mesotergata</i> (<i>L.</i>) <i>kirkwoodiana</i> (<i>L.</i>) <i>bernardinensis</i>	= Area P (Noonan 1990) <i>Harpalus martini</i> <i>Euxoa austini</i> <i>Pseudopsallus mohaviensis</i> <i>Apleurus hystrix</i>
2	So. Central Valley, California	(<i>E.</i>) <i>spinerecta</i> (<i>L.</i>) n.sp. nr. <i>mesotergata</i>	
3	So. Sierra Nevada	(<i>E.</i>) <i>baumanni</i> n. sp. (<i>E.</i>) <i>helpferi</i>	<i>Pseudopsallus enceliae</i>
4	No. Sierra Nevada	(<i>E.</i>) <i>leiocantha</i> (<i>E.</i>) <i>middlekauffi</i> (<i>L.</i>) <i>tenaya</i>	+ Area B in part (Noonan 1990) <i>Harpalus</i> sp. 1 <i>Euxoa juliae</i> <i>Hydraena tuolumne</i> <i>Pseudopsallus lattini</i>
5	N.W. Great Basin	(<i>E.</i>) <i>artemisiae</i> n. sp.	
6	N. E. Great Basin	(<i>E.</i>) <i>spaldingi</i> (<i>L.</i>) n. sp. nr. <i>mormon</i>	
7	E. Rim Great Basin	(<i>E.</i>) <i>eurystyla</i> (<i>E.</i>) <i>madina</i> (<i>E.</i>) <i>utahicola</i> (<i>E.</i>) <i>woodi</i>	
8	N. Colorado Plateau	(<i>E.</i>) <i>evalynae</i> n. sp. (<i>E.</i>) <i>kaibabensis</i> (<i>L.</i>) <i>mormon</i>	Area Q in part (Noonan 1990) <i>Harpalus corpulentus</i>
9	Mogollon Rim, Arizona	(<i>E.</i>) <i>dissipina</i> n. sp. (<i>E.</i>) <i>dimidiata</i> (<i>E.</i>) <i>mitrata</i> (<i>L.</i>) <i>mohavensis</i> (<i>L.</i>) sp. nr. <i>pleuracacula</i>	= Area O (Noonan 1990) <i>Harpalus cuncticeps</i> = Area I in part (Noonan 1990) <i>Harpalus retractus</i> <i>Capnura fibula</i> in part
10	S.E. Colorado Plateau	(<i>E.</i>) <i>anasazi</i> n. sp.	= Area N in part = Area I in part (Noonan 1990)
11	Santa Rita Mtns., Arizona	(<i>E.</i>) <i>kirkwoodi</i> (<i>E.</i>) <i>maderensis</i> n. sp.	
12	Huachuca Mtns., Arizona	(<i>E.</i>) <i>rogersi</i> n. sp.	= Area M <i>Harpalus huachuca</i> Area K in part (Noonan, 1990) = Area K in part (Noonan, 1990) <i>Hydraena bituberculata</i> = Area J (Noonan, 1990) <i>Harpalus cohni</i> <i>Apleurus parosus</i> <i>Ramentocoris baja</i> & <i>R. loreto</i>
13	N.W. Chihuahua Desert	(<i>L.</i>) <i>stalagmites</i>	
14	N. E. Chihuahua Desert	(<i>L.</i>) <i>polingi</i>	
15	S. Baja Peninsula	(<i>L.</i>) <i>lagunicola</i>	
16	N. C. California	(<i>L.</i>) <i>raysmithi</i> (<i>L.</i>) <i>lassenensis</i>	

References: all *Tipula* (Gelhaus 1989, this paper and unpublished); *Apleurus* (Anderson 1987); *Capnura* (Nelson & Baumann 1987); *Euxoa* (Lafontaine 1982); *Harpalus* (Noonan 1990); *Hydraena* (Perkins 1980); *Pseudopsallus* (Stonedahl & Schwarz 1986); *Ramentocoris* (Stonedahl & Schuh 1986).

Table 7. Allopatric Sister Species Disjunction Zones in *Tipula* (*Eremotipula*).

No.	Area-Area Disjunction Zone	Sister-Species Pair
1.	Area 11—Area 12	<i>kirkwoodi-rogersi</i>
2.	Area 2—Area 3	<i>helferi-spinerecta</i>
3.	Area 3—Area 7	<i>baumanni—utahicola</i>
4.	Area 8—Area 9	<i>kaibabensis—dimidiata</i>
5.	Area 9—Area 10	<i>mitrata—anasazi</i>
6.	Area 4,5,6,7,8—Area 1	<i>pellucida—schusteri</i> *
7.	Area 4,5,6,7,8—Area 4	<i>sinistra—middlekauffi</i>
8.	Pacific Coast (montane)—S. Rockies, SW Mountains	<i>sackeni—diversa</i>
9.	Area 4—Area 8	<i>leioanthra—evalynae</i> *

* = sister species under some phylogenetic reconstructions.

Welsh (1988) except for a lack of representation in the southern reaches of the track. The earliest lineages of *Eremotipula* are found in the Central Plains/Great Basin and Mojavean regions, respectively, and probably date from the Miocene or more recent, based on paleobotanical evidence of available habitat (Axelrod 1979). There are no fossils determinable to *Eremotipula*, so a minimum age based on fossil evidence cannot be established.

Subsequent cladogenesis formed two main lineages, the *eurystyla* species group and the "derived" species groups. The *eurystyla* species group shows an area relationship between southern Arizona and the southern Sierra Nevada, California, with these two areas related to the eastern rim of the Great Basin + southern Sierra Nevada, California. The "derived" species groups are primarily diverse in the Great Basin and Colorado Plateau regions, areas with endemic species in numerous other insect groups (Nelson 1994). Several Mojave-Great Basin disjunctions are seen (e.g. *biproducta* group, possibly *pellucida* and *schusteri*). The *diversa* and *madina* species groups show the more basal species on the Mogollon Rim or southern Colorado Plateau (*dispiina*, *jicarilla*), with subsequently more derived species occurring in the northern Colorado Plateau or Great Basin. The *kaibabensis* group has two species pairs, Mogollon Rim + Colorado Plateau (including Wasatch Range) and Mogollon Rim + north central New Mexico. This is in part congruent with the area relationships of the carabid subgenus *Harpalus* (*Glanodes*) except that a carabid species is found in west Texas, an area not inhabited by *Eremotipula*.

As noted, Noonan (1988) found limited congruence in reduced area cladograms among a wide variety of insects examined. The general relationship of areas shown by *Eremotipula* (Mojave + (Southern Basin and Range + Great Basin)) is partially congruent with that seen in one lineage of the mirid plant bug genus *Pseudopsallus* (Stone-dahl & Schwartz 1986) (Fig. 437).

EVOLUTION OF HABITAT USE IN *Eremotipula*

Due to the preliminary nature of the outgroup analysis, the most basal lineages of *Lunatipula* s. str. the sister group of *Eremotipula*, remain unidentified, but the mesic woodland and forest habitat used by the majority of species of *Lunatipula* s. str. is considered here as the groundplan condition (Gelhaus 1986). This habitat is not greatly different from that used by *incisa*, the sister species to the rest of the species of *Eremotipula*. Larvae of *incisa* occur in riparian woodlands in arid grasslands, where they feed on deciduous-tree leaf litter (similar to species of *Lunatipula*). This type of riparian habitat occurred in the Great Basin at least by the middle Pliocene (Axelrod 1950; Tidwell *et al.* 1972).

The evolution of this subgenus in the desert environments of the West appears to have started in the Mojave Desert region, starting with the splitting of the lineage leading to *incisa* from that leading to all of the other species. Following this initial speciation, several lineages developed in the Mojave leading to *larreae*, *melanderiana* and the *eurystyla* species group. Two of these species, *melanderiana* and *larreae*, can be found in southern

California today in semi-arid chaparral, pinyon-juniper woodland, or even extremely xeric desert scrub, where the larvae presumably feed on the sclerophyllous leaf litter accumulating under shrubs. During the Miocene, this same area supported live oak and pinyon pine woodland, along with areas of chaparral, and with patches of semi-desert vegetation possibly occurring on south-facing slopes (Axelrod 1979). An increase in aridity and in the extent of the desert vegetation likely occurred with the uplift of the Transverse Ranges west of the Mojave Desert during the Pliocene and Pleistocene. It seems likely then, that suitable habitats for the evolution of *Eremotipula* were available beginning in the Miocene, and were certainly prevalent during the Pliocene. The endemism of *Eremotipula* in western North America also tends to support an origin of the group no earlier than the Miocene. An important division occurred between the lineage leading to *macracantha* (a generally xeric species) from that leading to all of the derived species groups, of which nearly all occur in higher elevation, more mesic, semi-arid shrub habitats of the Great Basin and Colorado Plateau, and where the vast majority of species occur.

This finding that a progression towards the use of more xeric environments (i.e., ancestor $\rightarrow$ *incisa* $\rightarrow$ basal species) was, in fact, reversed in the lineage leading to the derived species groups may be corroborated in other desert groups, once their phylogenies are better known. For example, a similar situation may exist in the megachilid bee genus *Ashmeadiella* (Michener 1939), in which a montane species group (considered then in the subgenus *Titusella*) evolved from the primarily desert subgenus *Ashmeadiella* s. s. Several other aspects of the relationships within this bee genus present possible parallels to *Eremotipula*. The basal subgenus contains the only species widespread in eastern North America (similar in cladistic position and geographic distribution to *incisa* in *Eremotipula*), and the other subgenera have all "radiated" into the Great Basin from the Basin's western edge, similar to the diversification seen among the derived species groups of *Eremotipula*. A test of this congruence awaits a cladistic analysis of *Ashmeadiella*. In another group, LaFontaine (1982) considered that the ancestral stock of the noctuid moth genus *Euxoa* was probably adapted to open grassland and arid shrubland, with those

species found in montane forest habitats being more recently derived.

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LITERATURE CITED

- Alexander, C. P. 1918. New Nearctic crane-flies (Tipulidae, Diptera). Part VI. *The Canadian Entomologist* 50: 381-386, 411-416.
- Alexander, C. P. 1919. The crane-flies collected by the Canadian Arctic Expedition, 1913-1918. Pp. 3c-30c, in *Report of the Canadian Arctic Expedition 1913-1918*. Volume III: Insects. Part C: Diptera. J. de Labroquerie Taché, Ottawa. 1c-90c.
- Alexander, C. P. 1931. Crane-flies of the Baltic Amber (Diptera). *Bernstein-Forschungen* 2: 1-135.
- Alexander, C. P. 1942. Family Tipulidae. Pp. 196-486, in *Guide to the Insects of Connecticut*. Part VI. The Diptera or true flies of Connecticut. First Fascicle. External morphology; Key to families; Tanyderidae, Ptychopteridae, Trichoceridae, Anisopodidae, Tipulidae. Bulletin No. 64. State Geological and Natural History Survey, Hartford. i-x, 1-509.
- Alexander, C. P. 1945a. Records and descriptions of North American crane-flies (Diptera). Part V. Tipuloidea of the Grand Teton National Park and Teton National Forest, Wyoming. *The American Midland Naturalist* 33: 391-439.
- Alexander, C. P. 1945b. New Nearctic crane-flies (Tipulidae, Diptera). Part xxv. *The Canadian Entomologist* 77: 186-191.
- Alexander, C. P. 1946a. Records and descriptions of North American crane-flies (Diptera). Part VI. Tipuloidea of Arizona, New Mexico, and Trans-Pecos, Texas, 1. *The American Midland Naturalist* 35: 484-531.
- Alexander, C. P. 1946b. Undescribed species of *Tipula* from western North America (Diptera, Tipulidae). Part II. *Bulletin of the Brooklyn Entomological Society* 41: 45-51.
- Alexander, C. P. 1947. New Nearctic crane-flies (Tipulidae, Diptera): Part xxviii. *The Canadian Entomologist* 79: 68-73.
- Alexander, C. P. 1948. Records and descriptions of North American crane-flies. Part VII. The Tipuloidea of Utah, 1. *The American Midland Naturalist* 39: 1-82.
- Alexander, C. P. 1949. Records and descriptions of North American crane-flies (Diptera). Part VIII. The Tipuloidea of Washington, 1. *The American Midland Naturalist* 42: 257-333.
- Alexander, C. P. 1954. Records and descriptions of North American crane-flies (Diptera). Part ix. The Tipuloidea of Oregon, 1. *The American Midland Naturalist* 51: 1-86.
- Alexander, C. P. 1959. Undescribed species of Tipulidae from the western United States. Part V (Diptera). *The Pan-Pacific Entomologist* 35: 129-134.
- Alexander, C. P. 1961. Undescribed species of Nearctic Tipulidae (Diptera). 1. *The Great Basin Naturalist* 21: 79-86.
- Alexander, C. P. 1965a. New subgenera and species of crane-flies from California (Diptera: Tipulidae). *Pacific Insects* 7: 333-386.
- Alexander, C. P. 1965b. Family Tipulidae. Pp. 16-90, in Stone, A., Sabrosky, C. W., Wirth, W. W., Foote,

- R. H., and Coulson, J. R. (eds.). *A catalog of the Diptera of America north of Mexico*. Agricultural Research Service, United States Department of Agriculture, Washington, D.C. I-IV, 1-1696.
- Alexander, C. P. 1967. The crane flies of California. *Bulletin of the California Insect Survey* 8: 1-269.
- Alexander, C. P. 1969. Undescribed species of Nearctic Tipulidae (Diptera), x. *The Great Basin Naturalist* 29: 1-10.
- Alexander, C. P. & Byers, G. W. 1981. Tipulidae, Chapter 7. Pp. 153-190, in McAlpine, J. F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R., & Wood, D. M. (eds.). *Manual of Nearctic Diptera*. Volume 1. Monograph No. 27. Research Branch, Agriculture Canada, Ottawa. (4), i-vi, 1-674.
- Anderson, R. S. 1988. Systematics, phylogeny and biogeography of New World weevils traditionally of the tribe Cleonini (Coleoptera: Curculionidae; Cleoninae). *Quaestiones Entomologicae* 23: 431-709.
- Arnaud, P. H., Jr. 1979. A catalog of the types of Diptera in the collection of the California Academy of Sciences. *Myia* 1: i-vi, 1-505.
- Axelrod, D. I. 1950. Evolution of desert vegetation in western North America. Chapter VI, in *Studies in Late Tertiary paleobiology*. Carnegie Institution of Washington Publication 590. Carnegie Institution of Washington, Washington, D.C. (4), 1-323.
- Axelrod, D. I. 1979. Desert vegetation, its age and origin. Pp. 1-72, in Goodin, J. R. & Northington, D. K. (eds.). *Arid land plant resources*. International Center for Arid and Semi-arid Land Studies, Texas Tech University, Lubbock, Texas. (6), i-ii, 1-724.
- Brodo, F. 1987. A revision of the genus *Prionocera* (Diptera: Tipulidae). *Evolutionary Monographs* 8: 1-93.
- Brown, D. E. 1982a. 122.4. Great Basin conifer woodland. Pp. 52-57, in Brown, D. E. (ed.), *Biotic Communities of the American Southwest—United States and Mexico*. *Desert Plants* 4: 3-341.
- Brown, D. E. 1982b. 123.3. Madrean evergreen woodland. Pp. 59-65, in Brown, D. E. (ed.), *Biotic Communities of the American Southwest—United States and Mexico*. *Desert Plants* 4: 3-341.
- Byers, G. W. 1961. The crane fly genus *Dolichocheza* in North America. *University of Kansas Science Bulletin* 42: 665-924.
- Byers, G. W. 1976. Type specimens of Tipulidae described by R. W. Doane in the collection of the California Academy of Sciences. *Occasional Papers of the California Academy of Sciences* 124: 1-55.
- Carpenter, J. M. 1988. Choosing among multiple equally parsimonious cladograms. *Cladistics* 4: 291-296.
- Cracraft, J. 1988. Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. *Systematic Zoology* 37: 221-236.
- Crampton, G. C. 1942. The external morphology of the Diptera. Pp. 10-165, in *Guide to the Insects of Connecticut*. Part VI. The Diptera or true flies of Connecticut. First Fascicle. External morphology; Key to families; Tanyderidae, Ptychopteridae, Trichoceridae, Anisopodidae, Tipulidae. Bulletin No. 64. State Geological and Natural History Survey, Hartford. i-x, 1-509.
- Dietz, W. G. 1921. The *impudica* group of the dipterous genus *Tipula* Linnaeus. *Annals of the Entomological Society of America* 14: 1-14.
- Doane, R. W. 1901. Descriptions of new Tipulidae. *Journal of the New York Entomological Society* 9: 97-127.
- Doane, R. W. 1912. New western *Tipula*. *Annals of the Entomological Society of America* 5: 41-61.
- Dobrotworsky, N. V. 1968. The Tipulidae (Diptera) of Australia. I. A review of the genera of the subfamily Tipulinae. *Australian Journal of Zoology* 16: 459-494.
- Farris, J. A. 1988. *Hennig86, Version 1.5*. [computer software package]. Port Jefferson Station, New York.
- Fautin, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. *Ecological Monographs* 16: 252-310.
- Frommer, S. I. 1963. Gross morphological studies of the reproductive system in representative North American crane flies (Diptera: Tipulidae). *University of Kansas Science Bulletin* 44: 535-626.
- Gelhaus, J. K. 1986. Larvae of the crane fly genus *Tipula* in North America (Diptera: Tipulidae). *University of Kansas Science Bulletin* 53: 121-182.
- Gelhaus, J. K. 1989. Systematics and biogeography of the desert crane fly subgenus *Tipula* (*Eremotipula*). Ph.D. Dissertation, University of Kansas, Lawrence. 465 pp.
- Hemmingsen, A. M. 1956. Deep-boring ovipository instincts of some crane-fly species (Tipulidae) of the subgenera *Vestiplex* Bezzi and *Oreomyza* Pokorný and some associated phenomena. *Videnskabelige Meddelelser fra dansk naturhistorisk Forening* 118: 243-315.
- Hennig, W. 1966. *Phylogenetic systematics*. [Translated from German by Davis, D. D. & Zangerl, R]. University of Illinois Press, Urbana, Chicago, & London. (8), 1-263.
- Humphries, C. J. & Parenti, L. R. 1986. *Cladistic biogeography*. Clarendon Press, Oxford. i-xii, 1-98.
- Kavanaugh, D. H. 1979. Investigations on present climatic refugia in North America through studies on the distributions of carabid beetles: concepts, methodology and prospectus. Pp. 369-381, in Erwin, T. E., Ball, G. E. & Whitehead, D. R. (eds.). *Carabid beetles: Their evolution, natural history and classification*. Dr. W. Junk, The Hague, Boston, & London. (10), 1-635.
- Kavanaugh, D. H. 1980. Insects of western Canada, with special reference to certain Carabidae (Coleoptera): present distribution patterns and their origins. *The Canadian Entomologist* 112: 1129-1144.

- Kluge, A. J. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* 38: 7–25.
- Lafontaine, J. D. 1982. Biogeography of the genus *Euxoa* (Lepidoptera: Noctuidae) in North America. *The Canadian Entomologist* 114: 1–53.
- Maddison, W. P., Donoghue, M. J. & Maddison, D. R. 1984. Outgroup analysis and parsimony. *Systematic Zoology* 33: 83–103.
- Maddison, W. P. & Maddison, D. R. 1992. *MacClade: Analysis of phylogeny and character evolution. Version 3.0*. Sinauer Associates, Sunderland, Massachusetts.
- Mannheims, B. 1963. 15. Tipulidae [part]. Lieferung 238. Pp. 137–176, in Lindner, E. (ed). *Die Fliegen der palaearktischen Region*. Band III. E. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele), Stuttgart. 1–538.
- McAlpine, J. F. 1981. Morphology and terminology—adults. Chapter 2. Pp. 9–63, in McAlpine, J. F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R., & Wood, D. M. (eds.). *Manual of Nearctic Diptera*. Volume 1. Monograph No. 27. Research Branch, Agriculture Canada, Ottawa. (4), i–vi, 1–674.
- McKenzie, D. 1982. The northern Great Basin region. Pp. 67–82, in G. L. Bender (ed.). *Reference handbook on the deserts of North America*. Greenwood Press, Westport, Connecticut & London, England. i–xiv, 1–544.
- Michener, C. D. 1939. A revision of the genus *Aslmeadiella* (Hymen., Megachilidae). *The American Midland Naturalist* 22: 1–84.
- Minckley, W. L., Hendrickson, D. A. & Bond, C. E. 1986. Geography of western North American freshwater fishes: Description and relationships to intracontinental tectonism. Pp. 519–613, in Hocutt, & Wiley, E. O. (eds.). *The zoogeography of North American freshwater fishes*. John Wiley & Sons, New York, Chichester, Brisbane, Toronto & Singapore. i–xiv, 1–866.
- Mooney, H. A. 1973. Plant communities and vegetation. Pp. 7–17, in Lloyd, R. M. & Mitchell, R. S. (eds.). *A flora of the White Mountains, California and Nevada*. University of California Press, Berkeley, Los Angeles & London. (8), 1–202.
- Nelson, C. R. 1994. Insects of the Great Basin and Colorado Plateau. Chapter 10. Pp. 211–237, in K. T. Harper, K. T., St. Clair, L. L., Thorne, K. H. & Hess, W. M. (eds.). *Natural history of the Colorado Plateau and Great Basin*. University Press of Colorado, Niwot, Colorado. i–x, 1–294.
- Nelson, C. R. & Baumann, R. W. 1987. The winter stonefly genus *Capnura* (Plecoptera: Capniidae) in North America: systematics, phylogeny and zoogeography. *Transactions of the American Entomological Society* 113: 1–28.
- Nelson, G. & Platnick, N. I. 1981. *Systematics and biogeography. Cladistics and vicariance*. Columbia University Press, New York. i–xiv, 1–567.
- Nixon, K. C. & Carpenter, J. M. 1993. On outgroups. *Cladistics* 9: 413–426.
- Noonan, G. R. 1988. Biogeography of North American and Mexican insects, and a critique of vicariance biogeography. *Systematic Zoology* 37: 366–384.
- Noonan, G. R. 1990. Biogeographical patterns of North American *Harpalus* Latreille (Insecta: Coleoptera: Carabidae). *Journal of Biogeography* 17: 583–614.
- Neumann, H. 1958. Der Bau und die Funktion der männlichen Genitalapparate von *Trichocera annulata* Meig. und *Tipula paludosa* Meig. (Dipt. Nematocera). *Deutsche Entomologische Zeitschrift* 5: 236–298.
- Oosterbroek, P. 1980. The western palaearctic species of *Neplitoma* Meigen, 1803 (Diptera, Tipulidae), Part 5, phylogeny and biogeography. *Beaufortia* 29: 311–393.
- Pase, C. P. & Brown, D. E. 1982a. 122.3. Rocky Mountain (Petran) and Madrean Montane conifer forest. Pp. 43–48, in Brown, D. E. (ed.). *Biotic Communities of the American Southwest—United States and Mexico*. *Desert Plants* 4: 3–341.
- Pase, C. P. & Brown, D. E. 1982b. 133.3. Interior chaparral. Pp. 95–99, in Brown, D. E. (ed.). *Biotic Communities of the American Southwest—United States and Mexico*. *Desert Plants* 4: 3–341.
- Perkins, P. D. 1980. Aquatic beetles of the family Hydraenidae in the Western Hemisphere: classification, biogeography and inferred phylogeny (Insecta: Coleoptera). *Quaestiones Entomologicae* 16: 3–554.
- Peus, F. 1952. 17. Cylindrotomidae. Lieferung 169. In Lindner, E. (ed). *Die Fliegen der palaearktischen Region*. Band III. E. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele), Stuttgart. (4), 1–80.
- Pimentel, R. A. & Riggins, R. 1987. The nature of cladistic data. *Cladistics* 3: 201–209.
- Platnick, N. I. & Nelson, G. 1978. A method of analysis for historical biogeography. *Systematic Zoology* 27: 1–16.
- Rees, B. E. & Ferris, G. F. 1939. The morphology of *Tipula reesi* Alexander (Diptera: Tipulidae). *Microentomology* 4: 143–178.
- Riedel, M. P. 1913. Die palaarktischen Arten der Dipteren-Gattung *Tipula* L. *Abhandlungen des Vereins für Naturwissenschaftliche Erforschung des Niederrheins* 1: 1–222.
- Rogers, J. S. 1931. Notes on a small collection of crane-flies from Oklahoma, with description of new species: Tipulidae—Diptera. *Publications of the Oklahoma University Biological Survey* 3: 331–338.
- Sanderson, M. J. 1989. Confidence limits on phylogenies: The bootstrap revisited. *Cladistics* 5: 113–129.
- Savchenko, E. N. 1964. Crane-flies (Tipulidae). *Fauna U.S.S.R.*, Vol. 2, Pt. 4: 1–504 (in Russian).

- Savchenko, E. N. 1966. Phylogeny and systematics of the Tipulidae [in Russian]. *Fauna Ukraini* 14: 63–88. [German translation by Theowald, B. & Theischinger, G. 1979. *Tijdschrift voor Entomologie* 122: 91–126].
- Spaulding, W. G., Leopold, E. B., & Van Devender, T. R. 1983. Late Wisconsin paleoecology of the American Southwest. Pp. 259–293, in Wright, H. E., Jr. (ed.). *Late-Quaternary environments of the United States*. Volume 1 (Porter, S. C. (ed.)). The Late Pleistocene. University of Minnesota Press, Minneapolis. i–xiv, 1–407.
- Stry, J. 1968. Eine neue *Molophilus* Art aus der Slowakei (Diptera, Tipulidae). *Acta entomologica bohemoslovaca* 65: 239–240.
- Stry, J. 1976. *Eriocnopa* gen. n., with the description of a new species from Central Europe (Diptera, Tipulidae). *Acta entomologica bohemoslovaca* 73: 420–429.
- Stry, J. & Rozkošný, R. 1970. A revision of palaearctic species of the subgenera *Protophomyia* Alexander, *Ellipteroides* Becker and *Ptilostenodes* Alexander (Diptera, Tipulidae: *Gonomyia* Meigen). *Acta entomologica bohemoslovaca* 67: 362–374.
- Stonedahl, G. M. & Schuh, R. T. 1986. *Squamocoris* Knight and *Ramentomiris*, new genus (Heteroptera: Miridae: Orthotylinae). A cladistic analysis and description of seven new species from Mexico and the western United States. *American Museum Novitates* 2852: 1–26.
- Stonedahl, G. M. & Schwartz, M. D. 1986. Revision of the plant bug genus *Pseudopsallus* Van Duzee (Heteroptera: Miridae). *American Museum Novitates* 2842: 1–58.
- Swofford, D. L. 1993. *PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1*. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- Swofford, D. L. & Begle, D. P. 1993. *Phylogenetic Analysis Using Parsimony, Version 3.1, User's Manual*. Laboratory of Molecular Systematics, Smithsonian Institution, Washington, D.C. 1–257.
- Tangelder, I. R. M. 1985. Phylogeny of the *Nephrotoma dorsalis* species-group (Diptera, Tipulidae), mainly based on genitalic characters. *Beaufortia* 35: 135–174.
- Tangelder, I. R. M. 1988. The biogeography of the Holarctic *Nephrotoma dorsalis* species group (Diptera: Tipulidae). *Beaufortia* 38: 1–35.
- Teale, S. 1984. The genus *Tipula* (Diptera: Tipulidae) in the Southern Rocky Mountains. MSc. Thesis, University of Kansas, Lawrence. 127 pp.
- Theischinger, G. & Theowald, B. 1981. Katalog der Untergattung *Lunatipula* Edwards, 1931, s.l. (Diptera, Tipulidae, *Tipula* Linnaeus). *Verslagen en Technische Gegevens* 27: 1–55.
- Theowald, B. 1957. Die Entwicklungsstadien der Tipuliden (Diptera, Nematocera), insbesondere der West-Palaarktischen Arten. *Tijdschrift voor Entomologie* 100: 195–308.
- Theowald, B. & Oosterbroek, P. 1990. Zur Zoogeographie der Westpalaarktischen Tipuliden. IX. Die Tipuliden des Vorderen Orients. *Tijdschrift voor Entomologie* 133: 85–95.
- Tidwell, W. D., Rushforth, S. R., & Simper, D. 1972. Evolution of floras in the intermountain region. Pp. 19–37, in A. Cronquist, Holmgren, A. H., Holmgren, N. H., & Reveal, J. L. (eds.). *Intermountain Flora. Vascular plants of the intermountain west, U.S.A.* Volume 1. The New York Botanical Garden & Hafner Publishing Company, New York & London. (6), i–vi, 1–270.
- Tjeder, B. 1958. A synopsis of the Swedish Tipulidae. 1. Subfam. Limoniinae: tribe Limoniini. *Opuscula Entomologica* 23: 133–169.
- Turner, R. M. 1982. 453.1. Mohave Desertscrub. Pp. 157–168, in Brown, D. E. (ed.). Biotic Communities of the American Southwest—United States and Mexico. *Desert Plants* 4: 3–341.
- Turner, R. M. & Brown, D. E. 1982. Sonoran Desertscrub. Pp. 181–221, in Brown, D. E. (ed.). Biotic Communities of the American Southwest—United States and Mexico. *Desert Plants* 4: 3–341.
- Van Devender, T. R., Thompson, R. S., & Betancourt, J. L. 1987. Vegetation history of the deserts of southwestern North America; the nature and timing of the Late Wisconsin-Holocene transition. In Ruddiman, W. F. and Wright, H. E., Jr. (eds.). *North America and adjacent oceans during the last deglaciation* Vol. K-3. Geological Society of America, Boulder, Colorado.
- Vane-Wright, R. I. 1967. A re-assessment of the genera *Holorusia* Loew (= *Ctenacrosceles* Enderlein), *Ischnotoma* Skuse and *Zelandotipula* Alexander (Diptera: Tipulidae), with notes on their phylogeny and zoogeography. *Journal of Natural History* 4: 511–547.
- Vasek, F. C. & Barbour, M. G. 1977. Mohave Desert scrub vegetation. Pp. 835–867, in Barbour, M. G. & Major, J. (eds.). *Terrestrial Vegetation of California*. John Wiley & Sons, New York, London, Sydney & Toronto. i–xii, 1–1002.
- Watrous, L. E. & Wheeler, Q. D. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30: 1–11.
- Wells, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecological Monographs* 53: 341–382.
- Welsh, H. H., Jr., 1988. An ecogeographic analysis of the herpetofauna of the Sierra San Pedro Martir region, Baja California, with a contribution to the biogeography of the Baja California herpetofauna. *Proceedings of the California Academy of Sciences* 46: 1–72.
- Wiley, E. O. 1981. *Phylogenetics. The theory and practice of phylogenetic systematics*. John Wiley and Sons, New York, Chichester, Brisbane & Toronto. i–xvi, 1–439.

- Young, C. W. & Gelhaus, J. K. 1992. *Leptotarsus* (*Longurio*) *byersi*, a new flightless crane fly from Ecuador (Diptera: Tipulidae). *Acta zoologica cracoviensia* **35**: 97–105.
- Young, J. A., Evans, R. A. & Major, J. 1977. Sagebrush steppe. Pp. 763–796, in Barbour, M. G. & Major, J. (eds.). *Terrestrial Vegetation of California*. John Wiley & Sons, New York, London, Sydney & Toronto. i–xii, 1–1002.

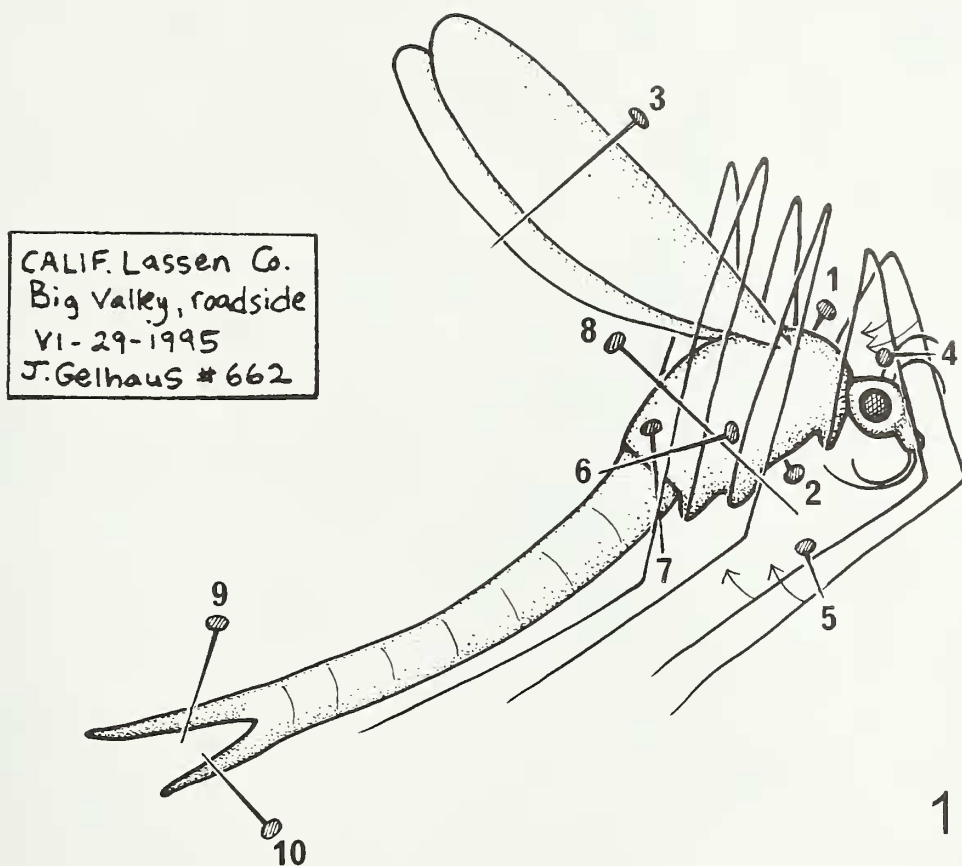
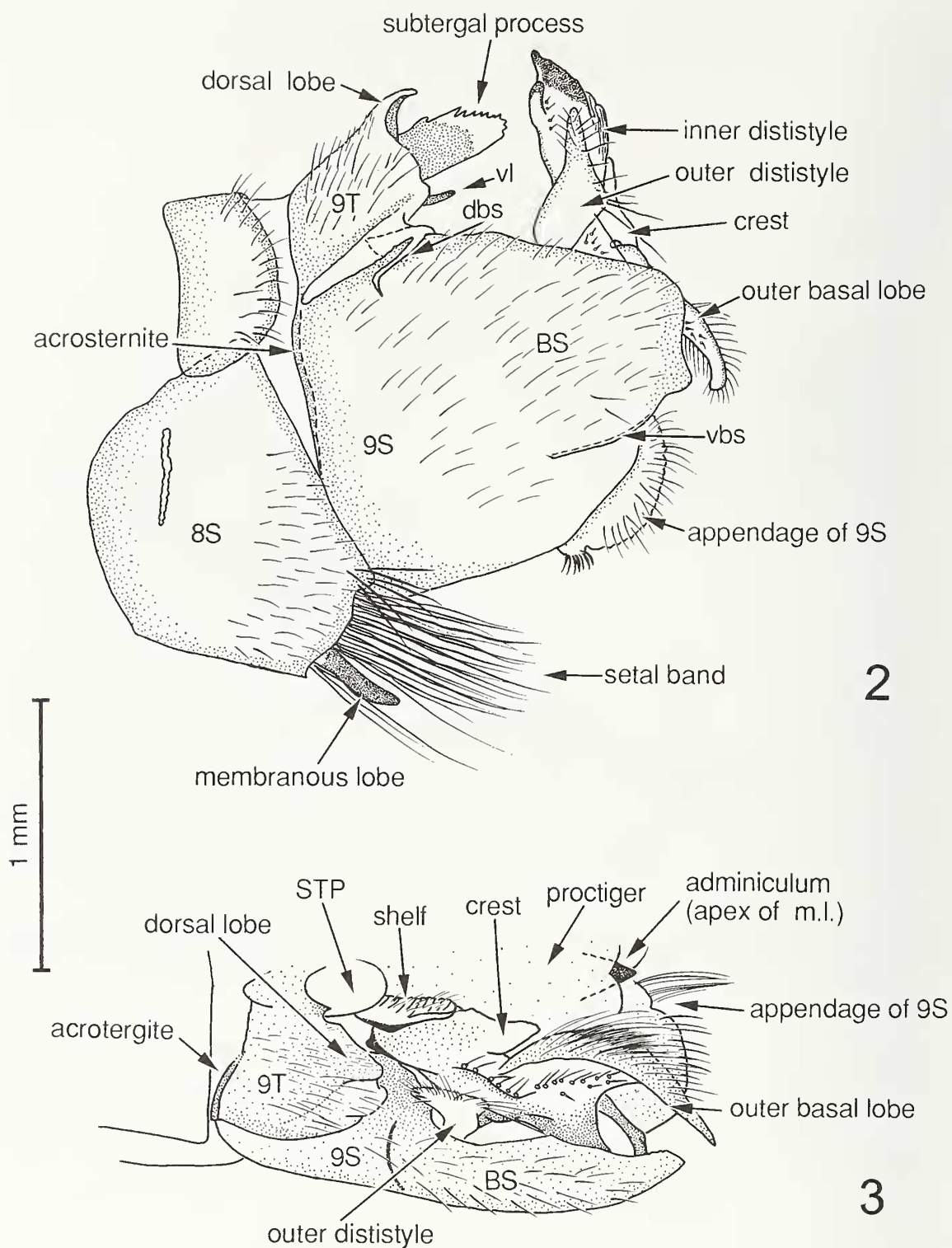
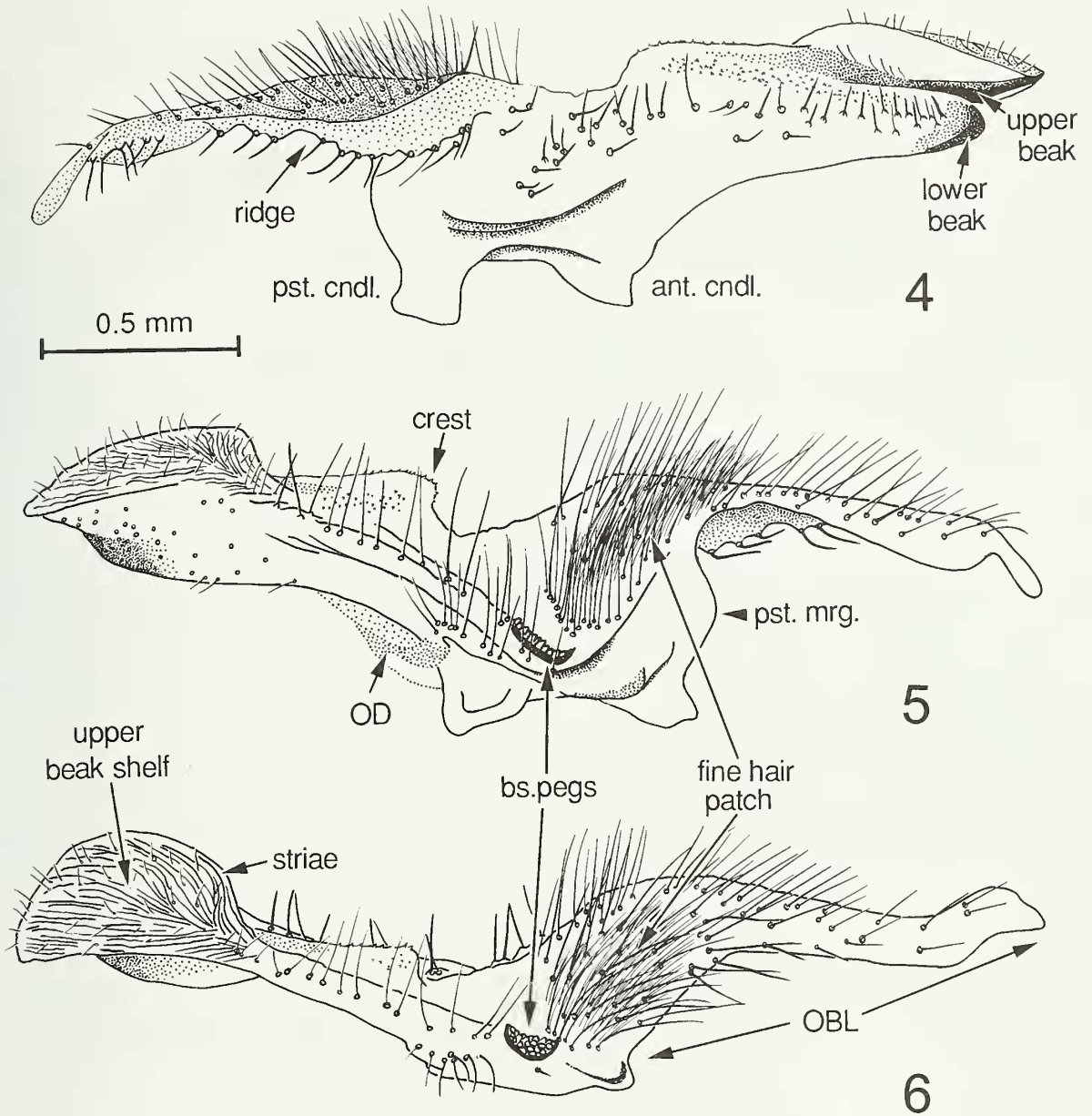


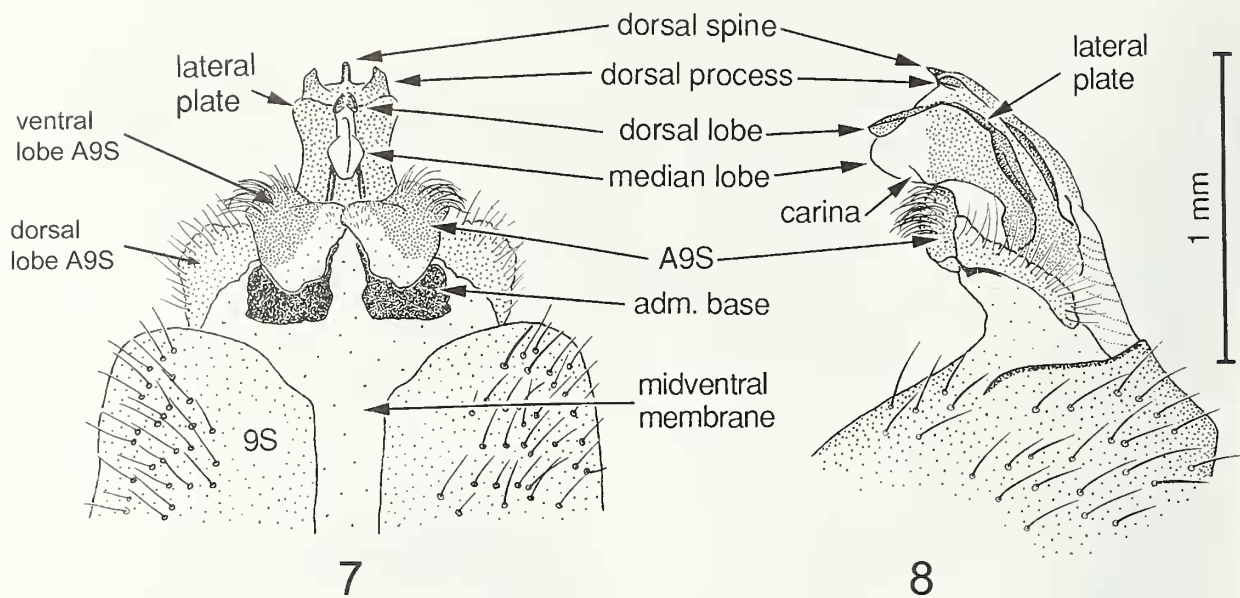
Fig. 1. Field pinning technique for female *Tipula* (*Eremotipula*) to allow for easier examination of genitalia. Pin numbers refer to order of pinning.



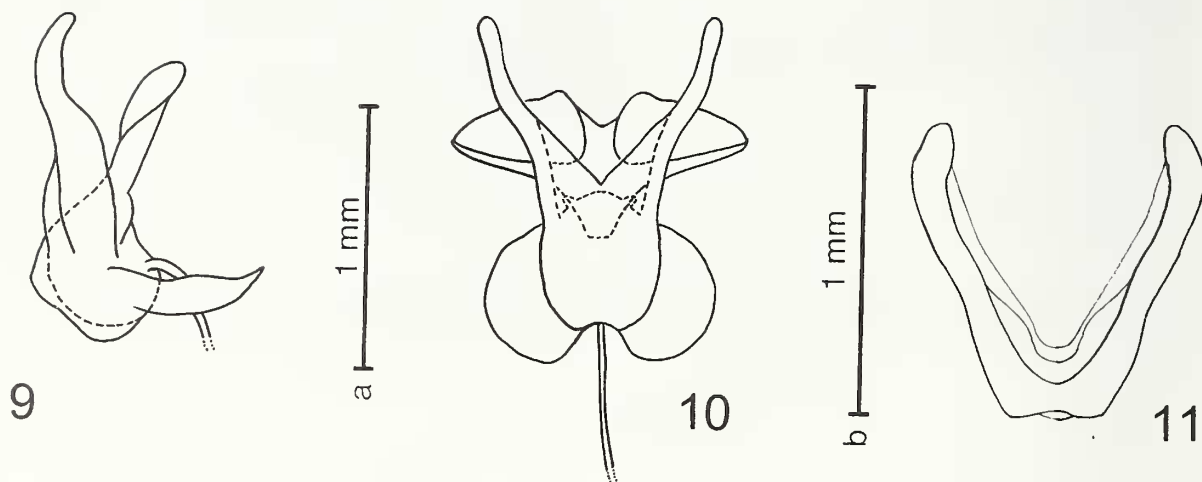
Figs. 2-3. 2, *Tipula (Eremotipula) spinosa*, lateral view. *dbs* = dorsal portion of basistylar suture. *vbs* = ventral portion of basistylar suture. *vl* = ventral lobe of 9T. 3, *T. (E.) pellucida*, male hypopygium, dorsal view. *ml* = median lobe.



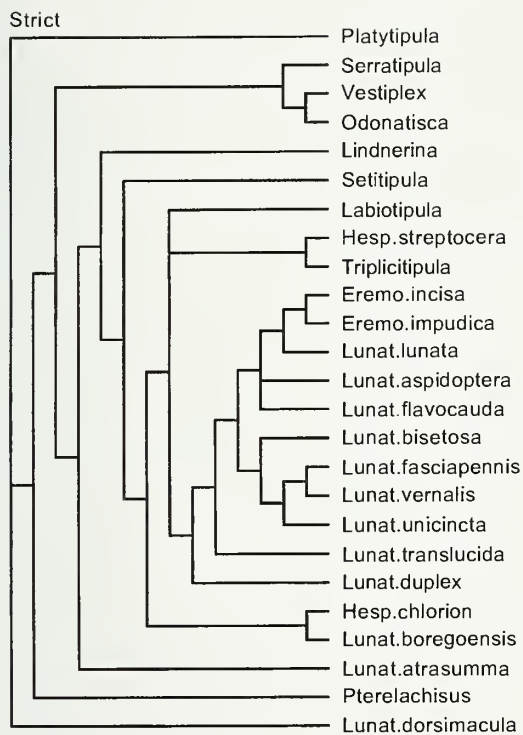
Figs. 4-6. *Tipula (Eremotipula) sackeni*, male inner dististyle. 4, lateral aspect. *ant. cndl.* = anterior condyle, *pst. cndl.* = posterior condyle. 5, mesal aspect. *pst. mrg.* = posterior margin. 6, dorsal aspect. *bs. pegs* = basiconic pegs.



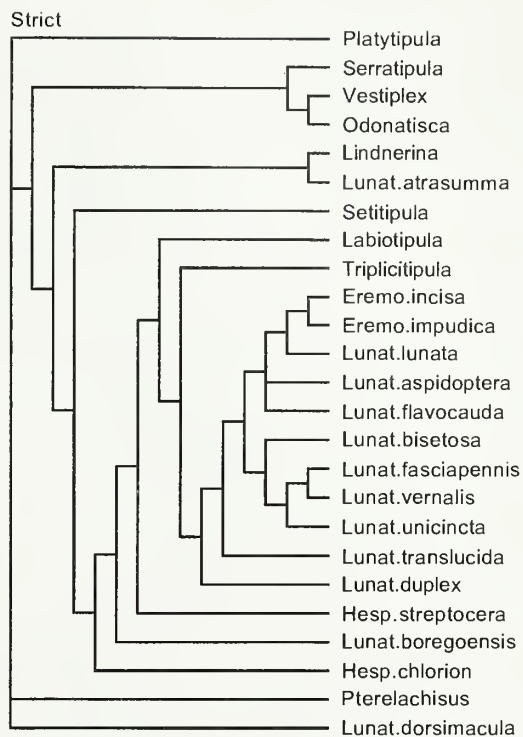
Figs. 7–8. *Tipula* (*Eremotipula*) *kaibabensis*, male ninth sternum. 7, ventral aspect. *adm.* = adminiculum. 8, lateral aspect.



Figs. 9–11. *Tipula* (*Eremotipula*) *diversa*, male. 9, vesica, lateral aspect. 10, vesica, anterior aspect. 11, sp1 (part of genital bridge). Scale a: 9, 10; scale b: 11.



12



13

Figs. 12-13. 12, Strict consensus tree of 6 SACW trees from ordered-character, phylogenetic analysis for the *Lunatipula-Vestiplex* group of subgenera of *Tipula*. 13, Strict consensus tree of 9 SACW trees from unordered-character, phylogenetic analysis for the *Lunatipula-Vestiplex* group of subgenera of *Tipula*.

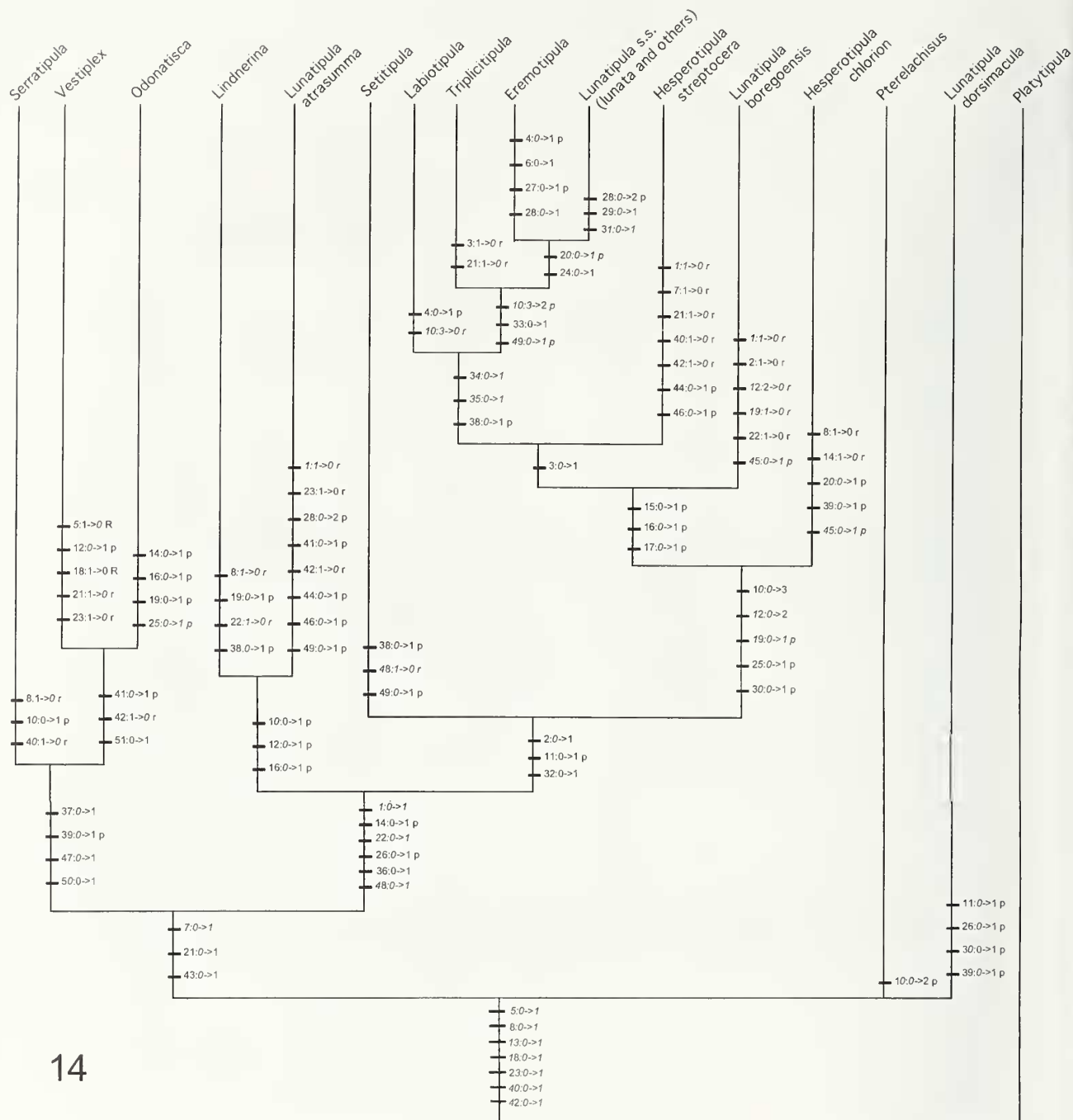
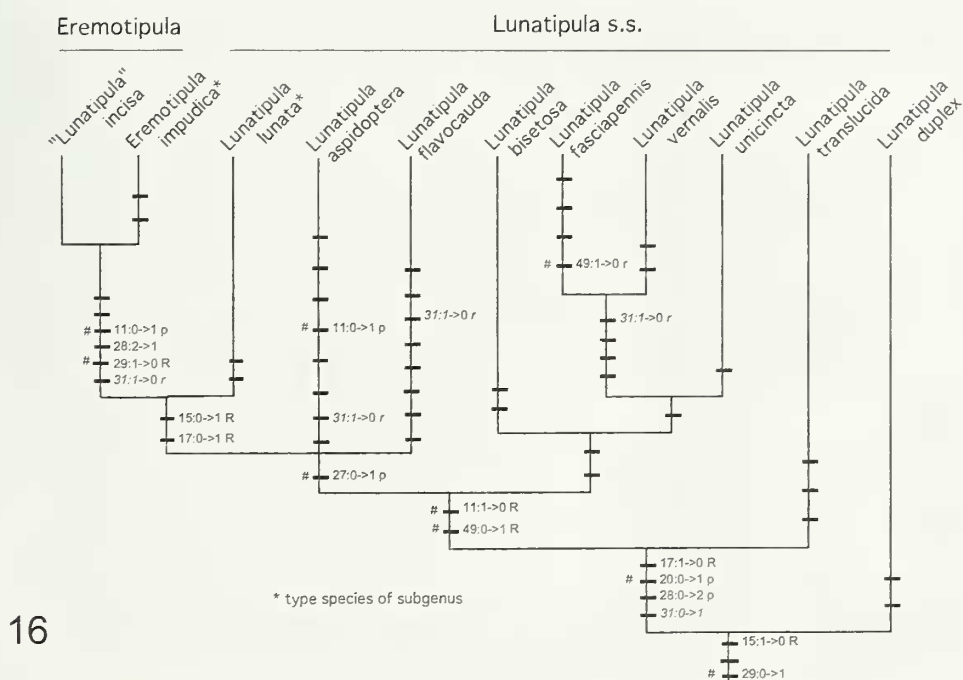
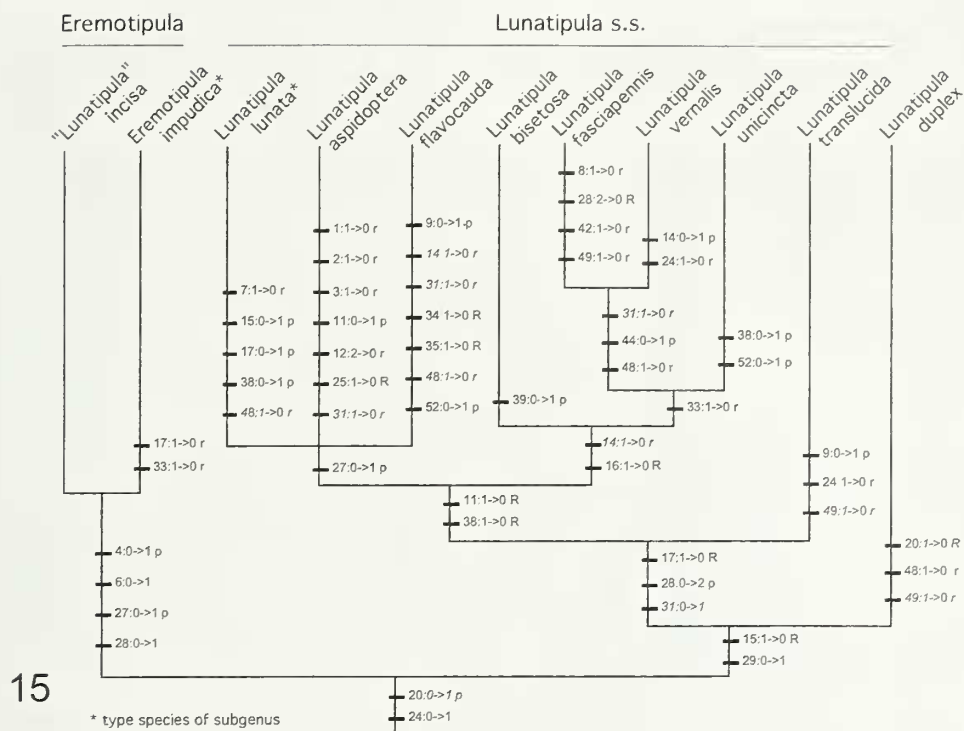
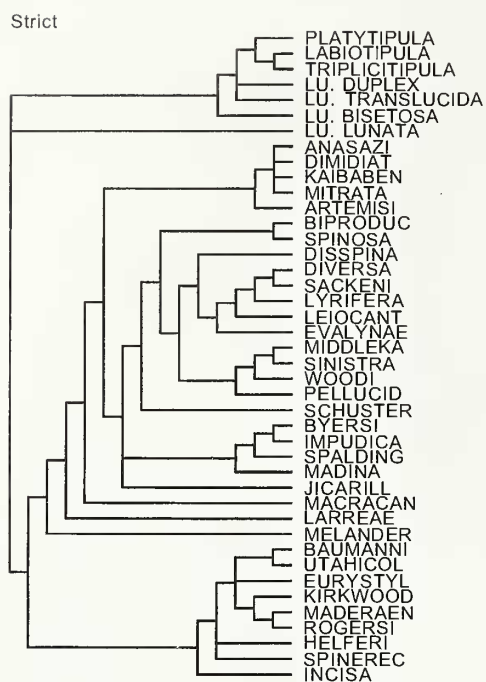


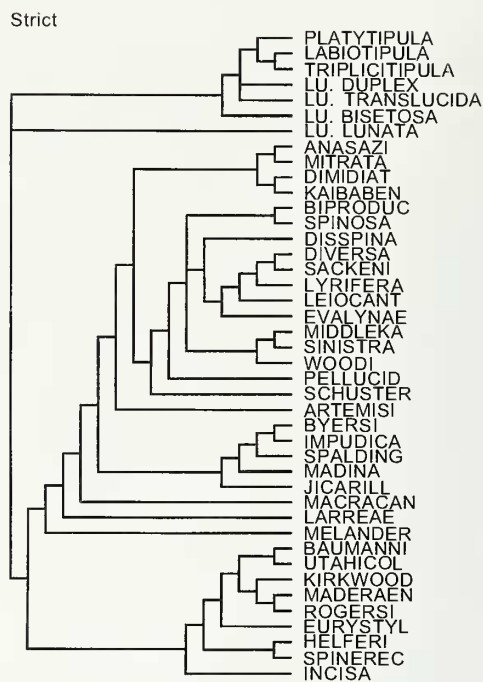
Fig. 14. Preferred cladogram for the phylogenetic analysis of the *Lunatipula-Vestiplex* group of subgenera of *Tipula*. All character changes are plotted. Tree length is one step more than most parsimonious. Character changes in normal text are unambiguous; italics imply other equally parsimonious changes are possible. r = multiple reversal. R = single reversal in character. p = parallelism.



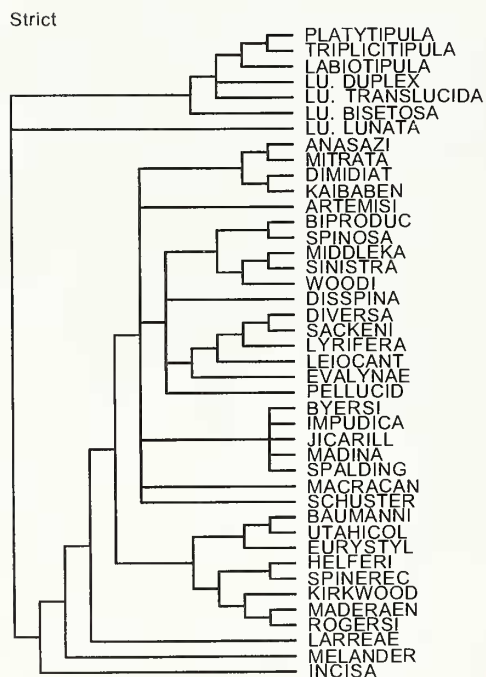
Figs. 15–16. Detailed relationships of *Tipula* (*Eremotipula*) and *Tipula* (*Lunatipula*) s.s. 15, Preferred topology, tree length one step more than most parsimonious. All character changes plotted. 16, One of the equally parsimonious cladograms. Only character changes differing from Fig. 15 are plotted. Character changes in normal text are unambiguous; italics imply other equally parsimonious changes are possible. r = multiple reversal. R = single reversal in character. p = parallelism.



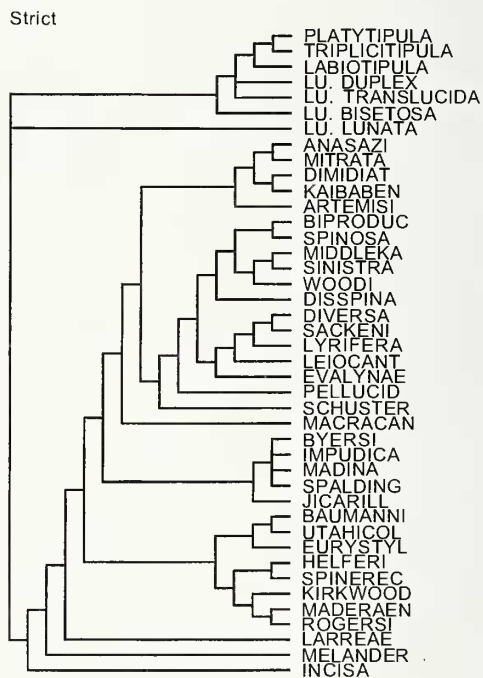
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Figs. 17–20. Strict consensus trees for phylogenetic analysis of the species relationships of *Tipula* (*Eremotipula*). 17, consensus tree of 12 trees from ordered-character, unweighted analysis. 18, consensus tree of 3 trees from SACW from ordered character analysis. 19, consensus tree of 32 trees from unordered character, unweighted analysis. 20, consensus tree of 6 trees from SACW from unordered character analysis.

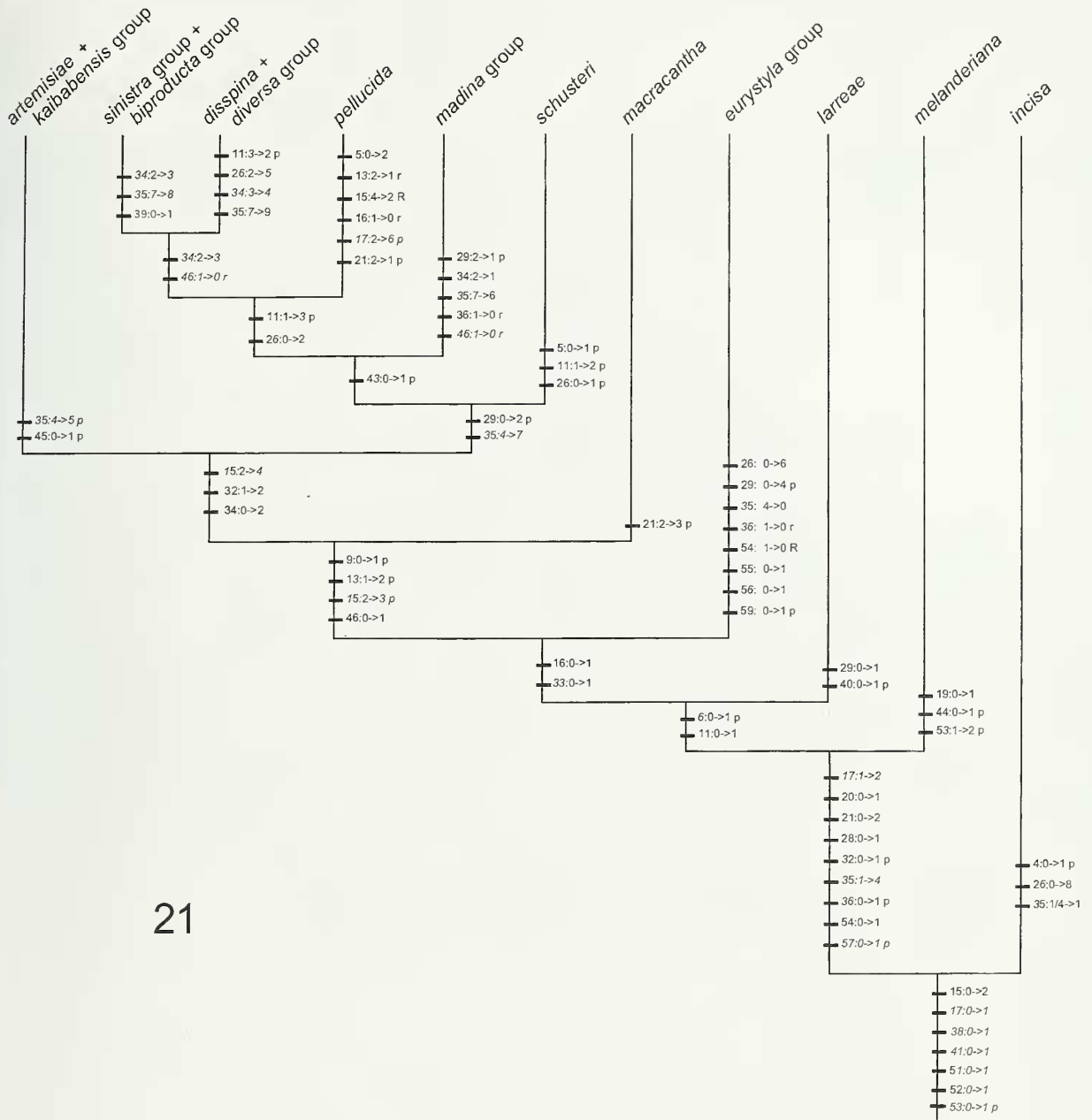
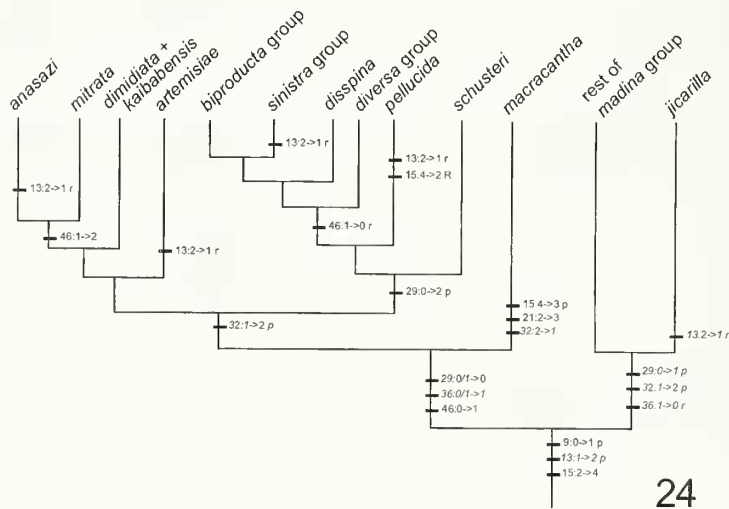
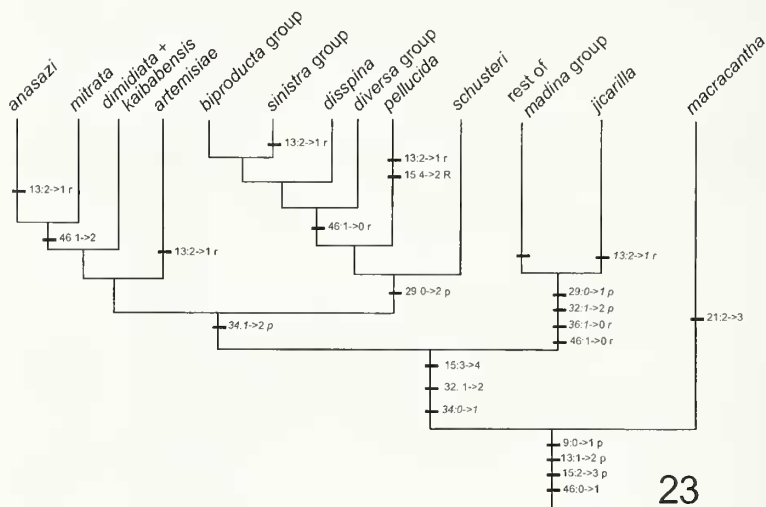
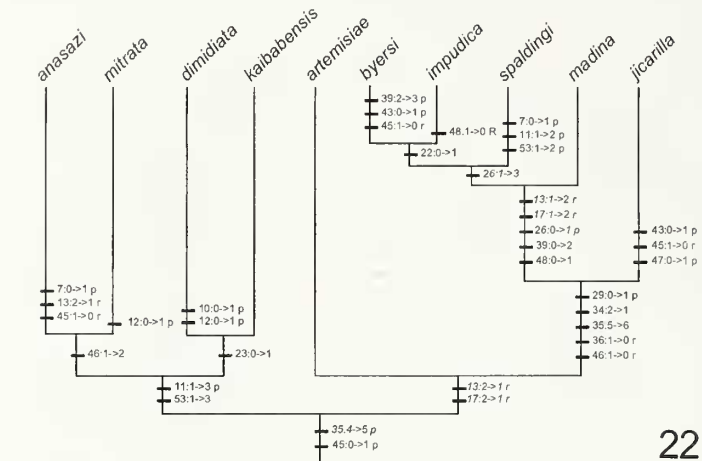
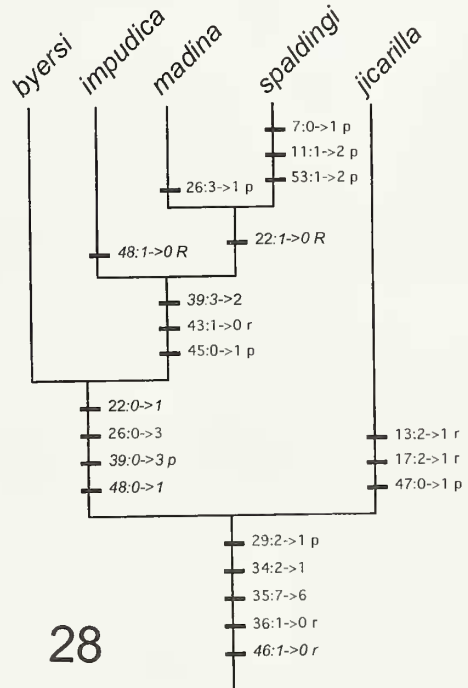
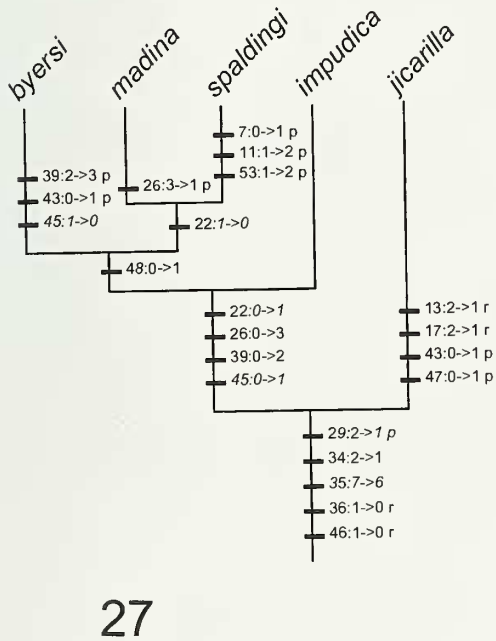
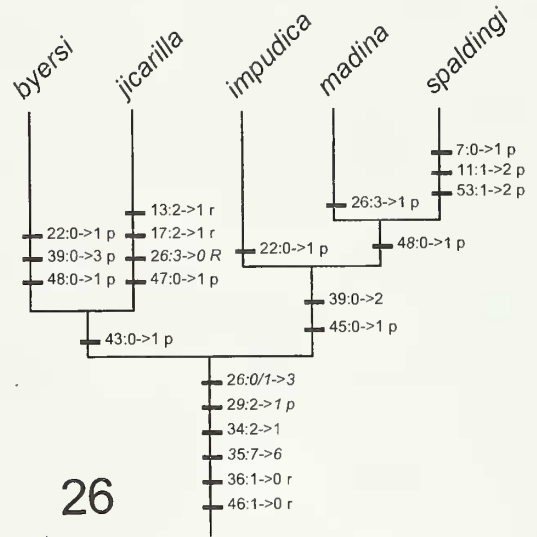
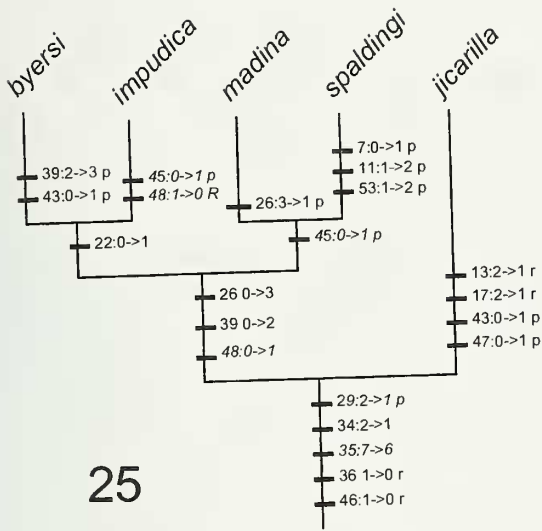


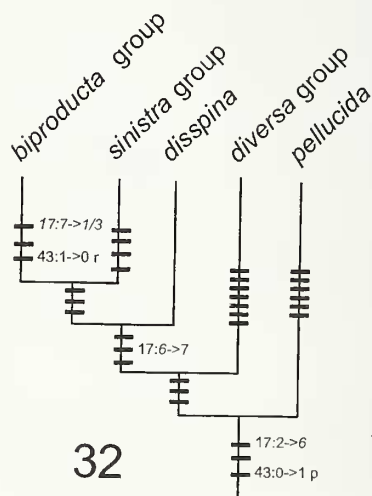
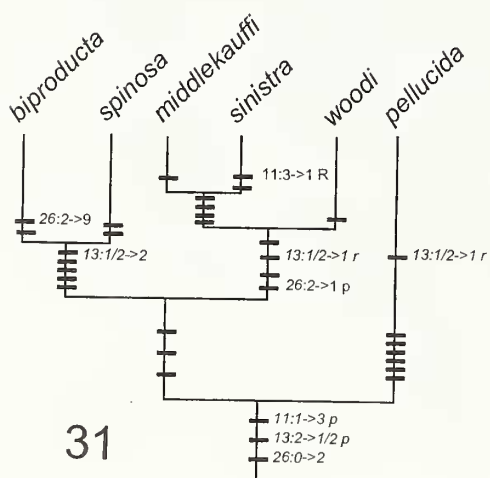
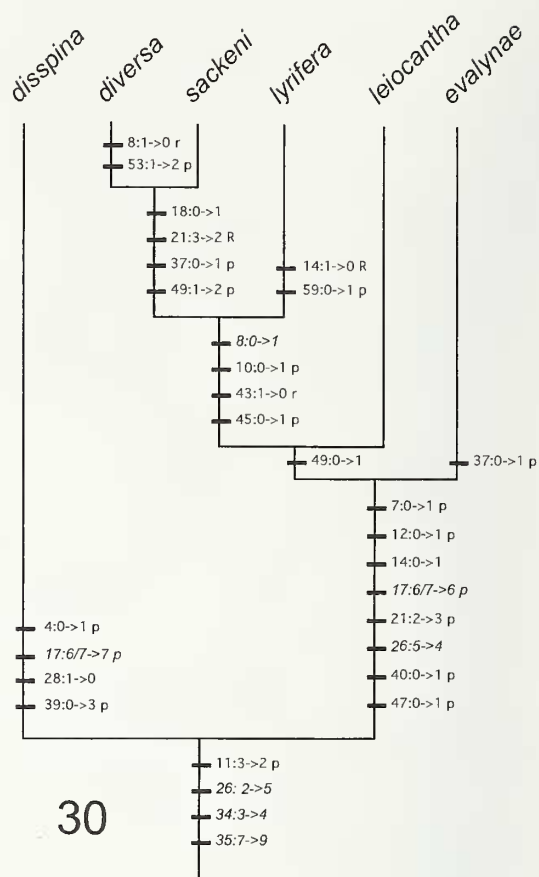
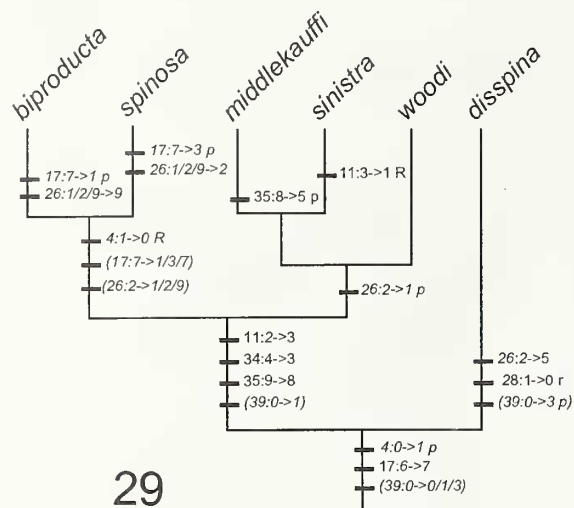
Fig. 21. Preferred tree from set of 32 minimal length trees from unordered-character, unweighted phylogenetic analysis of the species relationships of *Tipula* (Eremotipula): Components A1, C2, D1, F4 present.



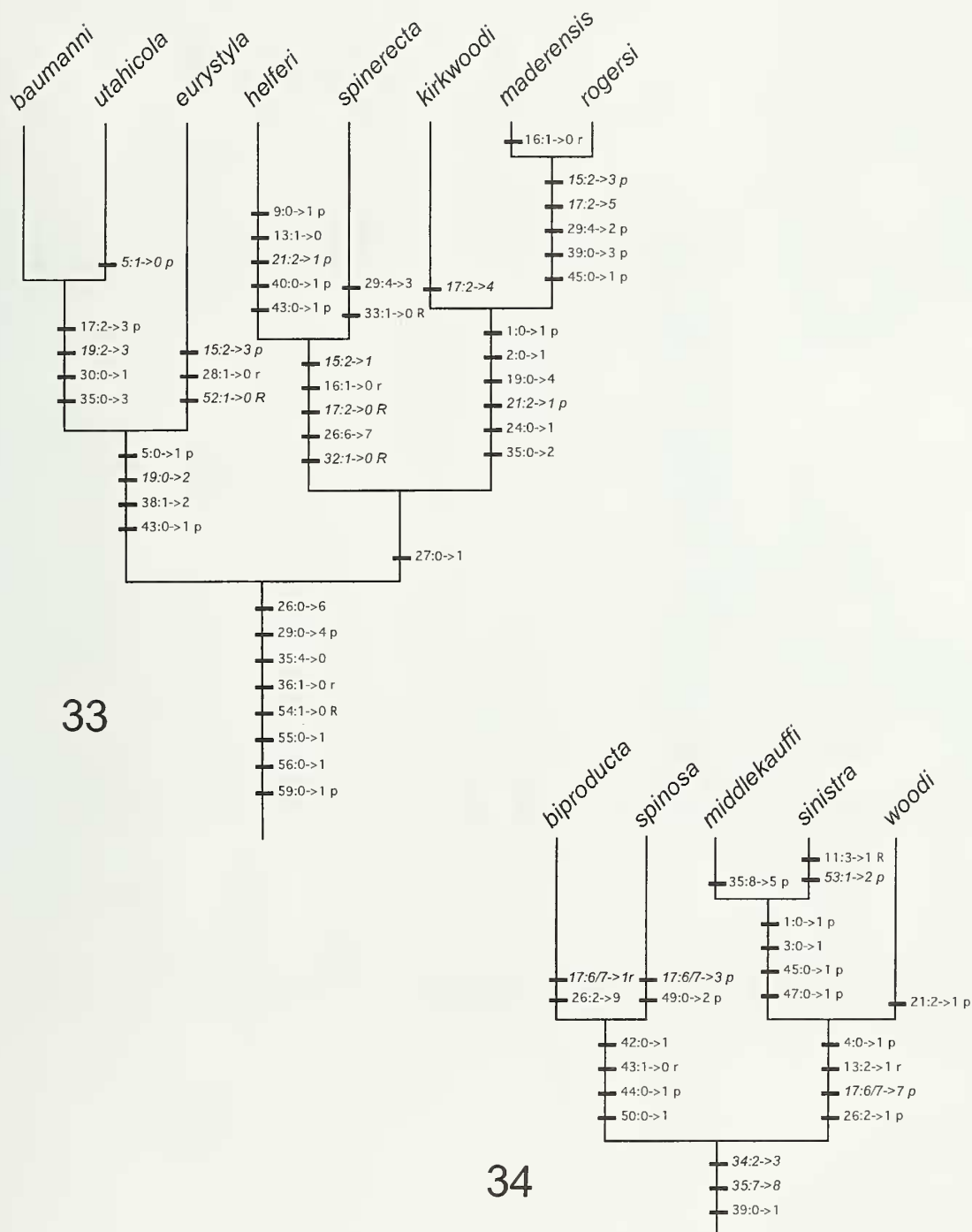
Figs. 22–24. Variable components of the 32 minimal length trees from unordered-character, unweighted phylogenetic analysis of the species relationships of *Tipula* (*Eremotipula*). 22, Components A2, B2, F1 present. 23, Component F2. 24, Component F3



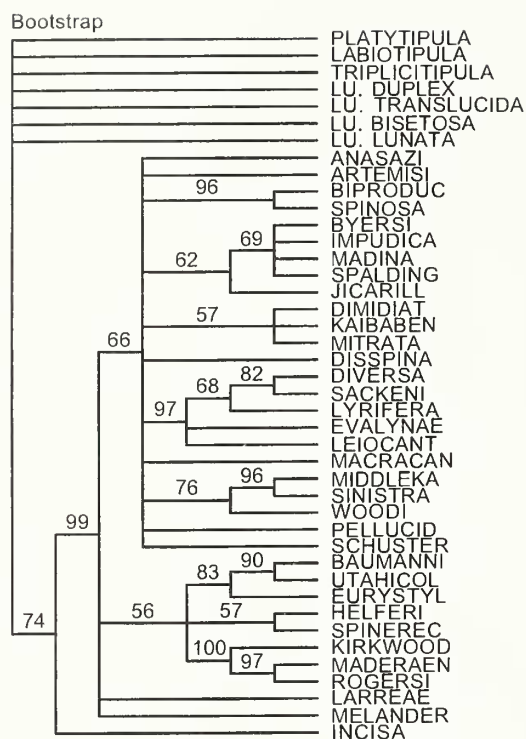
Figs. 25–28. Variable components of the 32 minimal length trees from unordered-character, unweighted phylogenetic analysis of the species relationships of *Tipula* (*Eremotipula*). Resolution of the *impudica* species group (Component B2 in Fig. 22). 25, Component B1. 26, Component B3. 27, Component B4. 28, Component B5.



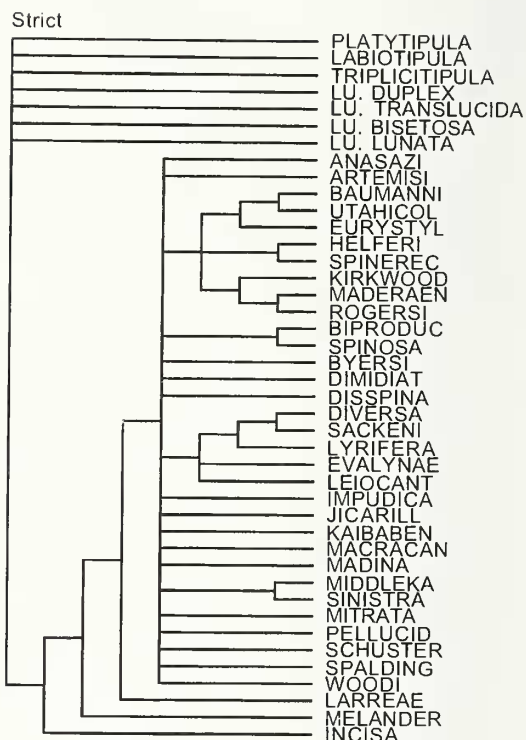
Figs. 29–32. Variable components of the 32 minimal length trees from unordered-character, unweighted phylogenetic analysis of the species relationships of *Tipula* (*Eremotipula*). 29, Component C1. 30, Component C2. 31, Component D2, only relevant character changes shown. 32, Component D3, only relevant characters changes shown.



Figs. 33–34. 33, resolution of *eurystyla* species group from unordered-character, unweighted phylogenetic analysis of the species relationships of *Tipula* (*Eremotipula*). 34, resolution of *sinistra* and *biproducta* species groups from unordered-character, unweighted phylogenetic analysis of the species relationships of *Tipula* (*Eremotipula*).

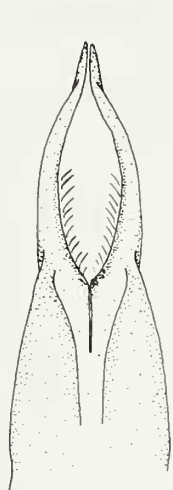


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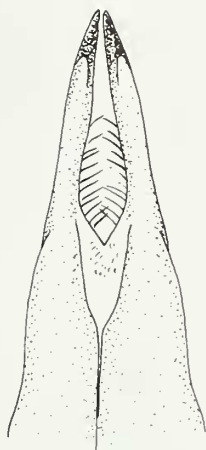


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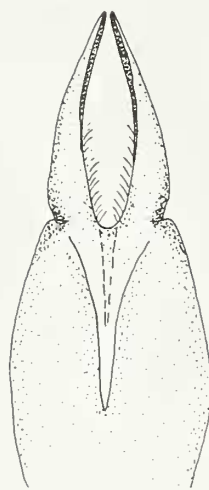
Figs. 35–36. 35, bootstrap values after 100 replications for unordered-character, phylogenetic analysis of the species relationships of *Tipula* (*Eremotipula*). 36, consensus tree of minimal and near minimal trees for unordered-character, phylogenetic analysis of the species relationships of *Tipula* (*Eremotipula*).



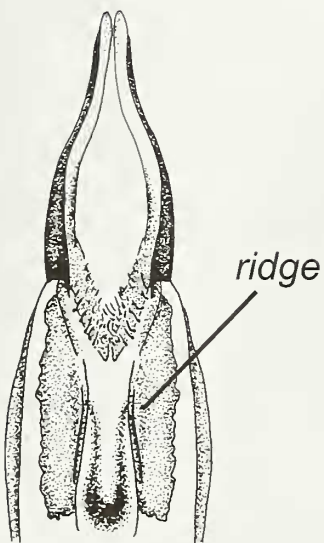
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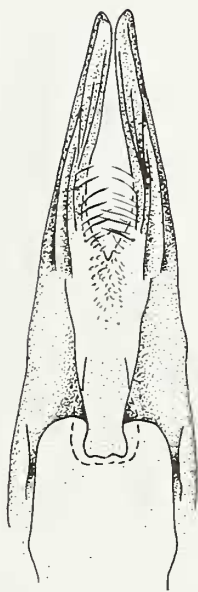
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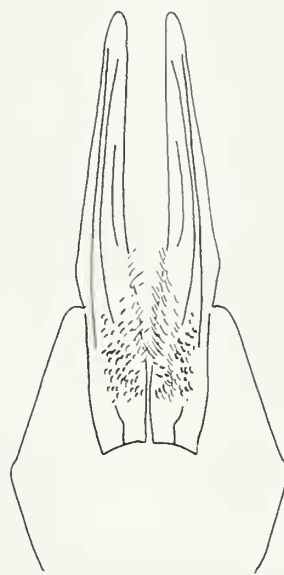
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Figs. 37–42. *Tipula*, female, eighth sternum. 37 and 40, *Tipula* (*Eremotipula*) *kaibabensis*, ventral and dorsal views. 38 and 41, *Tipula* (*Triplicitipula*) sp., ventral and dorsal views. 39 and 42, *Tipula* (*Lunatipula*) sp., ventral and dorsal views.

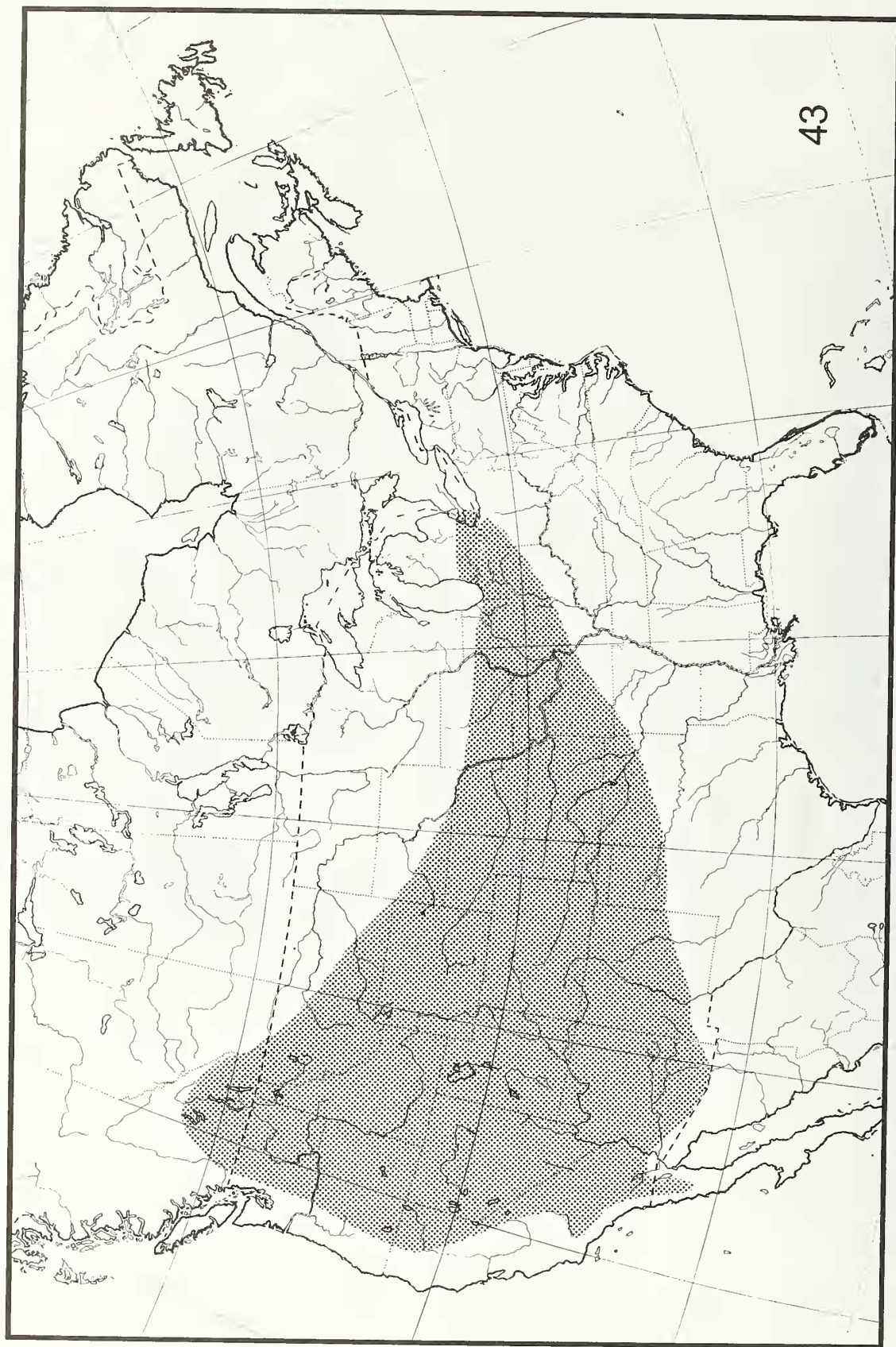
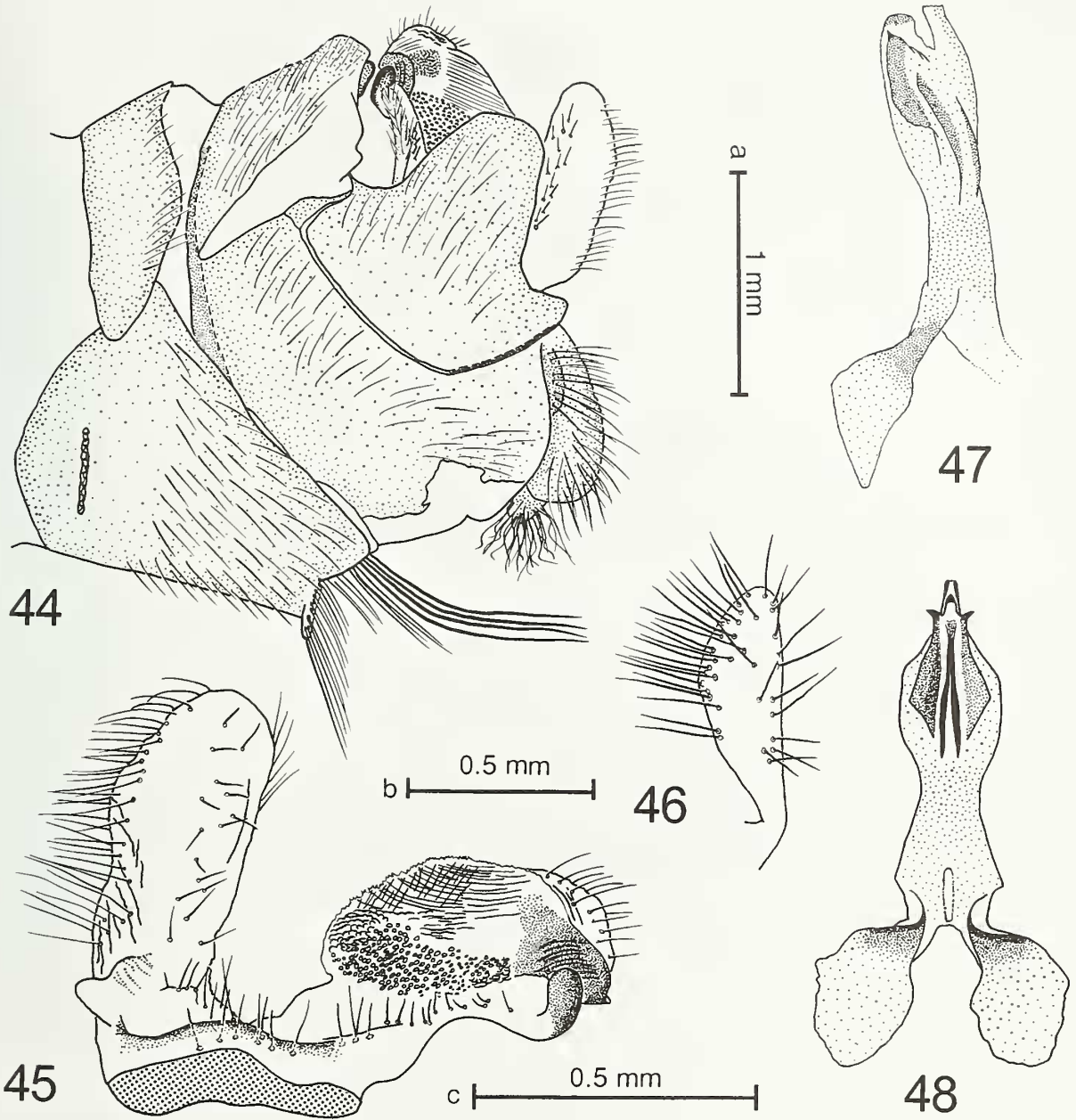
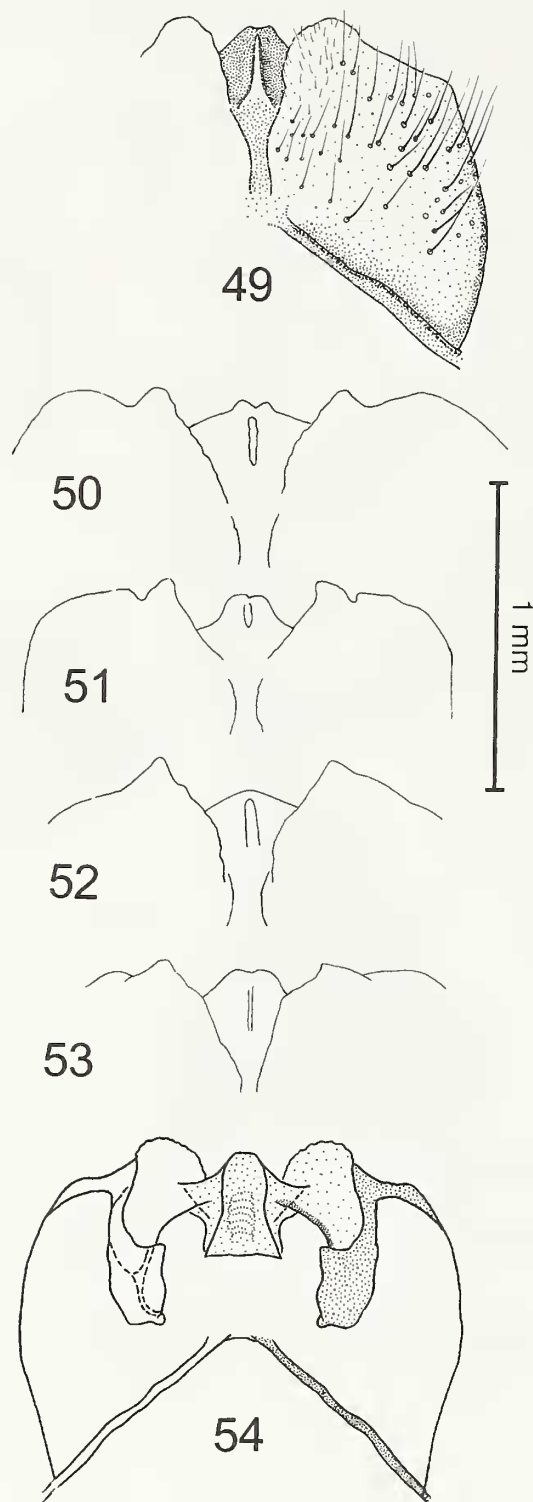


Fig. 43. Map showing distribution of the subgenus *Tipula* (*Eremotipula*).

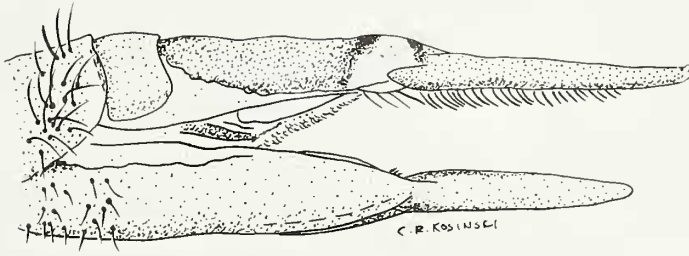


Figs. 44–48. *Tipula (Eremotipula) incisa*, features of male terminalia. 44, hypopygium, lateral aspect. 45, inner dististyle, lateral aspect. 46, outer dististyle, lateral aspect. 47, adminiculum, posterodorsal aspect. Scale a: 44; b, 45; c, 46, 47, 48.

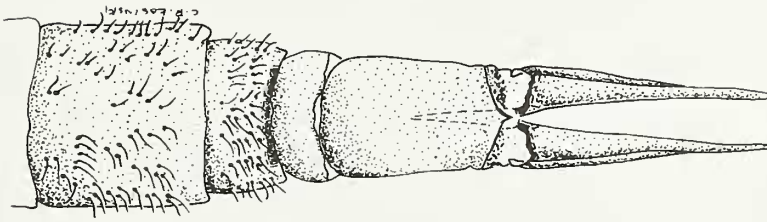


Figs. 49-54. *Tipula (Eremotipula) incisa*, male ninth tergum. 49, dorsal view, Oklahoma. 50- 53, dorsal outlines. 50, British Columbia. 51, New Mexico. 52, lectotype, Washington. 53, Kansas. 54, ventral view.

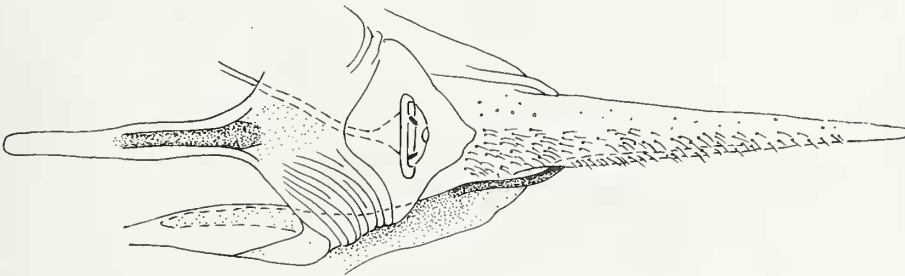
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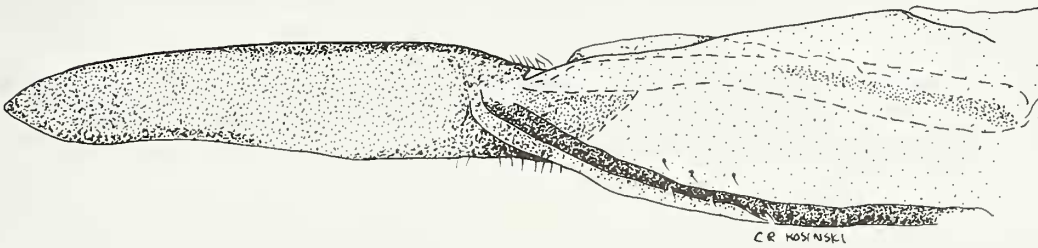
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58



Figs. 55–58. *Tipula (Eremotipula) incisa*, female genitalia. 55, lateral view. 56, dorsal view. 57, fused valvulae and vaginal apodeme. 58, lateral view of hypogynial valves and eighth sternum.

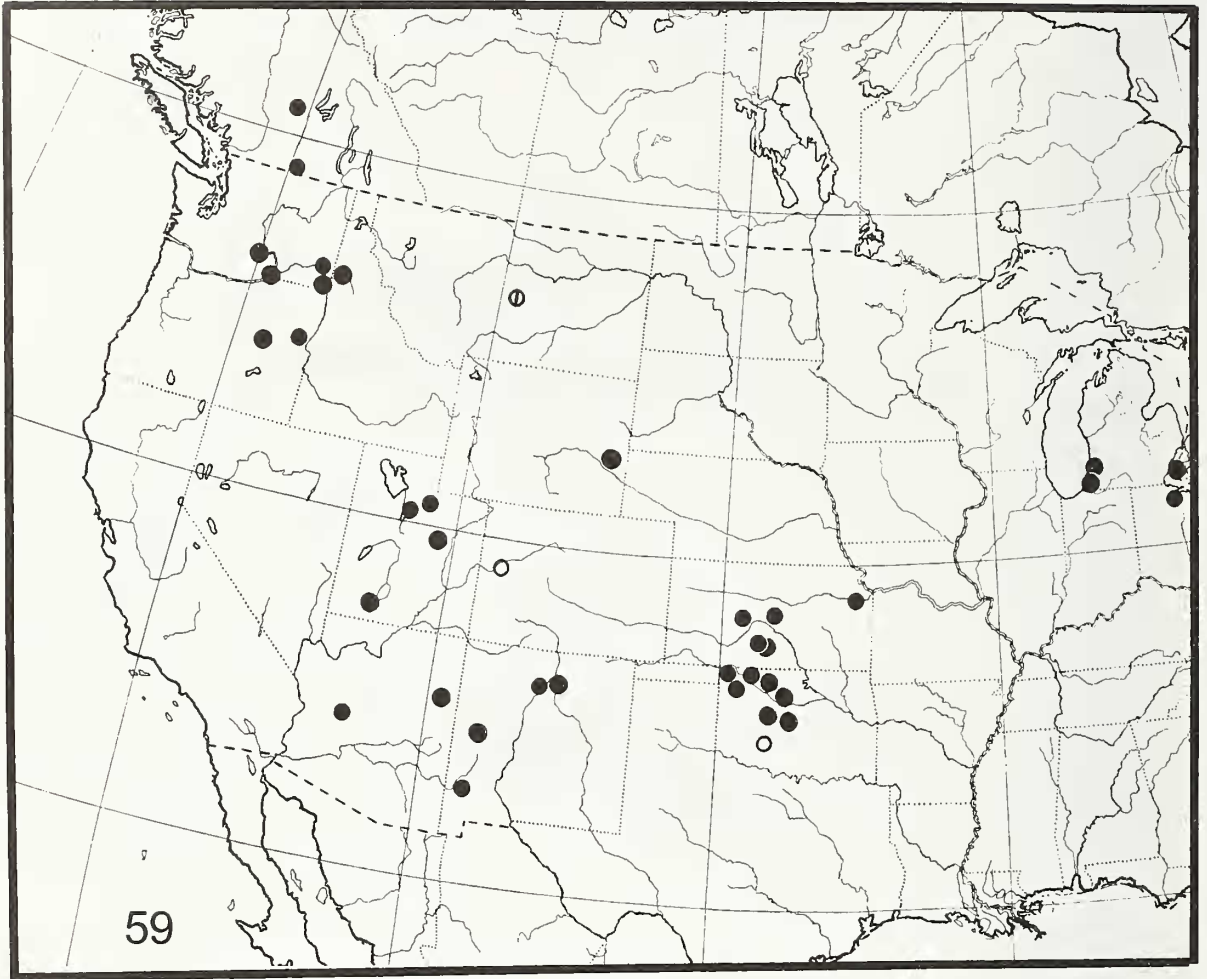
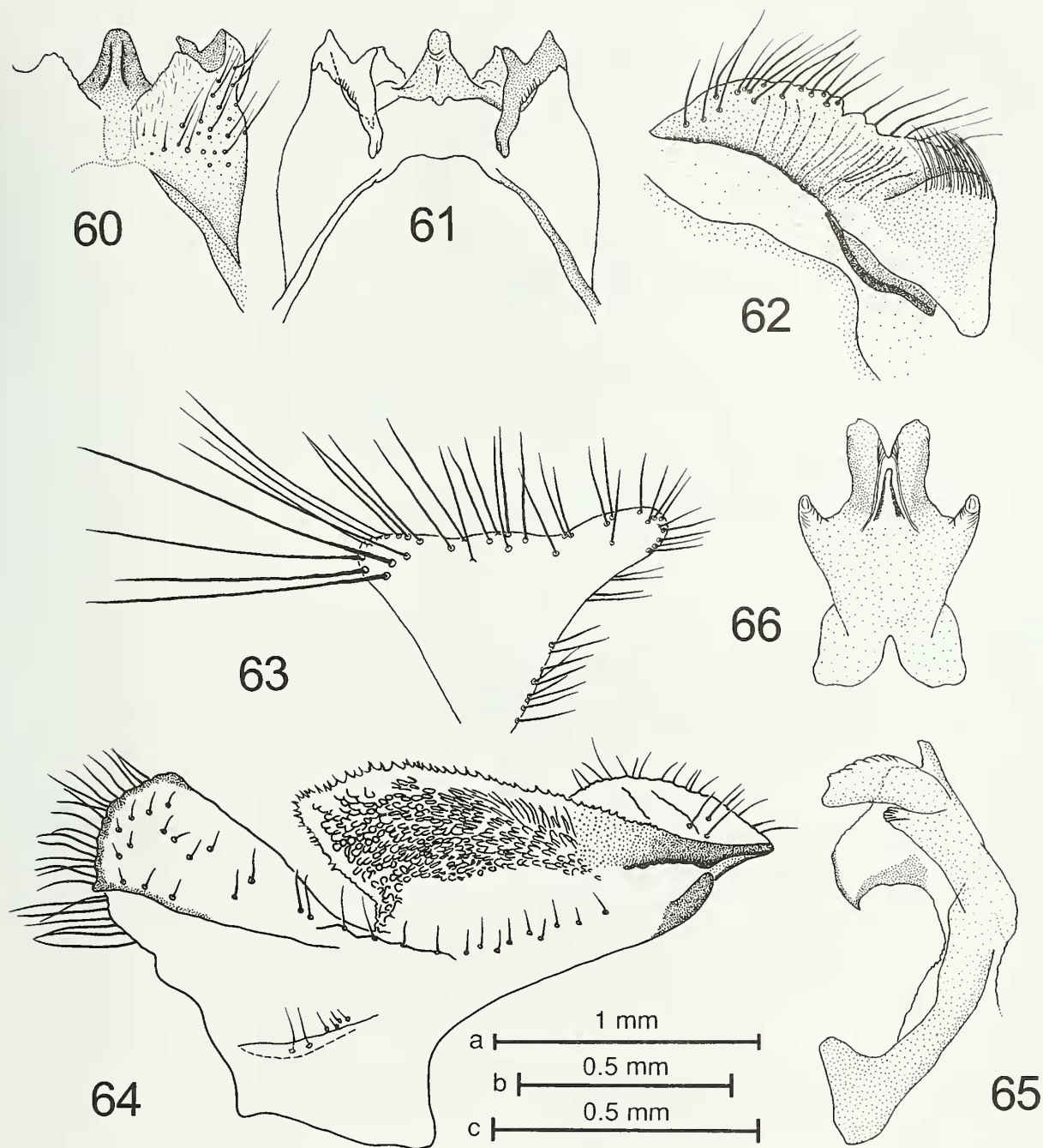
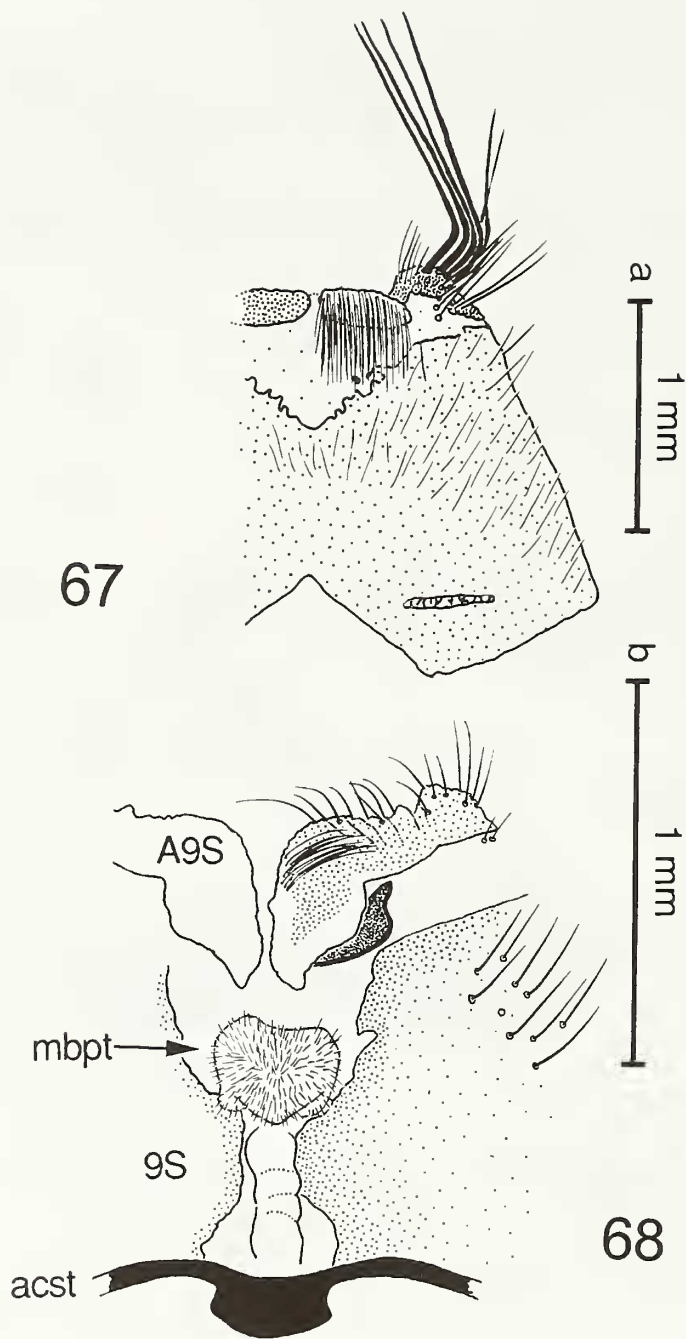


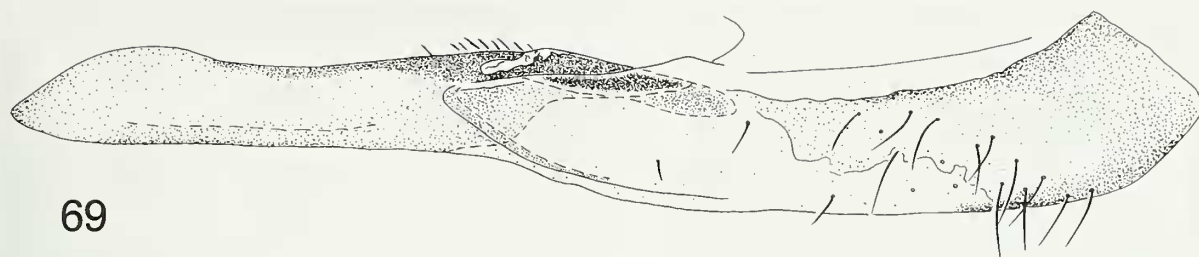
Fig. 59. Distribution of *Tipula (Eremotipula) incisa* Doane. Black circles represent localities of specimens examined in this study, white circles represent those localities previously published, and the single bisected circle is a state record (Montana) without further locality data.



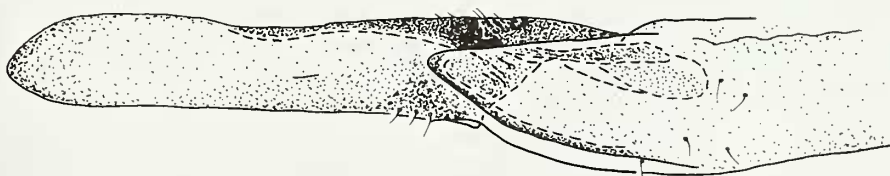
Figs. 60–66. *Tipula (Eremotipula) melanderiana*, male. 60, ninth tergum, dorsal view. 61, ninth tergum, ventral view. 62, appendage of ninth sternum, lateral view. 63, outer dististyle, lateral view. 64, inner dististyle, lateral view. 65, 66, adminiculum, lateral and dorsal views. Scale: a, 60–61; b, 62, 65–66; c, 63–64.



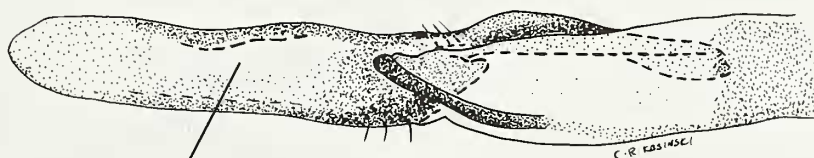
Figs. 67–68. *Tipula* (*Eremotipula*) *melanderiana*, male. 67, eighth sternum. 68, ninth sternum, ventral view; *acst* = acrosternite, *mbpt* = membranous protuberance. Scale a: 67; scale b: 68.



69

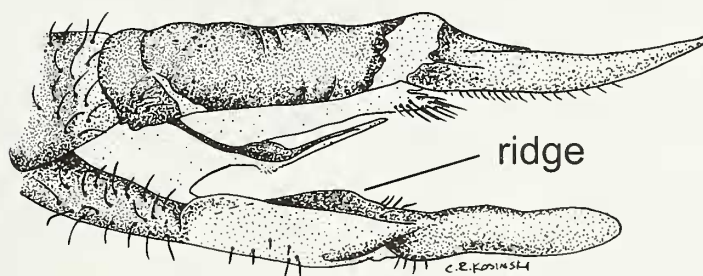


70



71

pale area



ridge

72

Figs. 69–72. Female genitalia. 69, 70, *Tipula (Eremotipula) larreae*, lateral view of hypogynial valves and eighth sternum. 71–72, *Tipula (Eremotipula) melanderiana*. 71, lateral view of hypogynial valves and eighth sternum 72, lateral view of terminal abdominal segments.

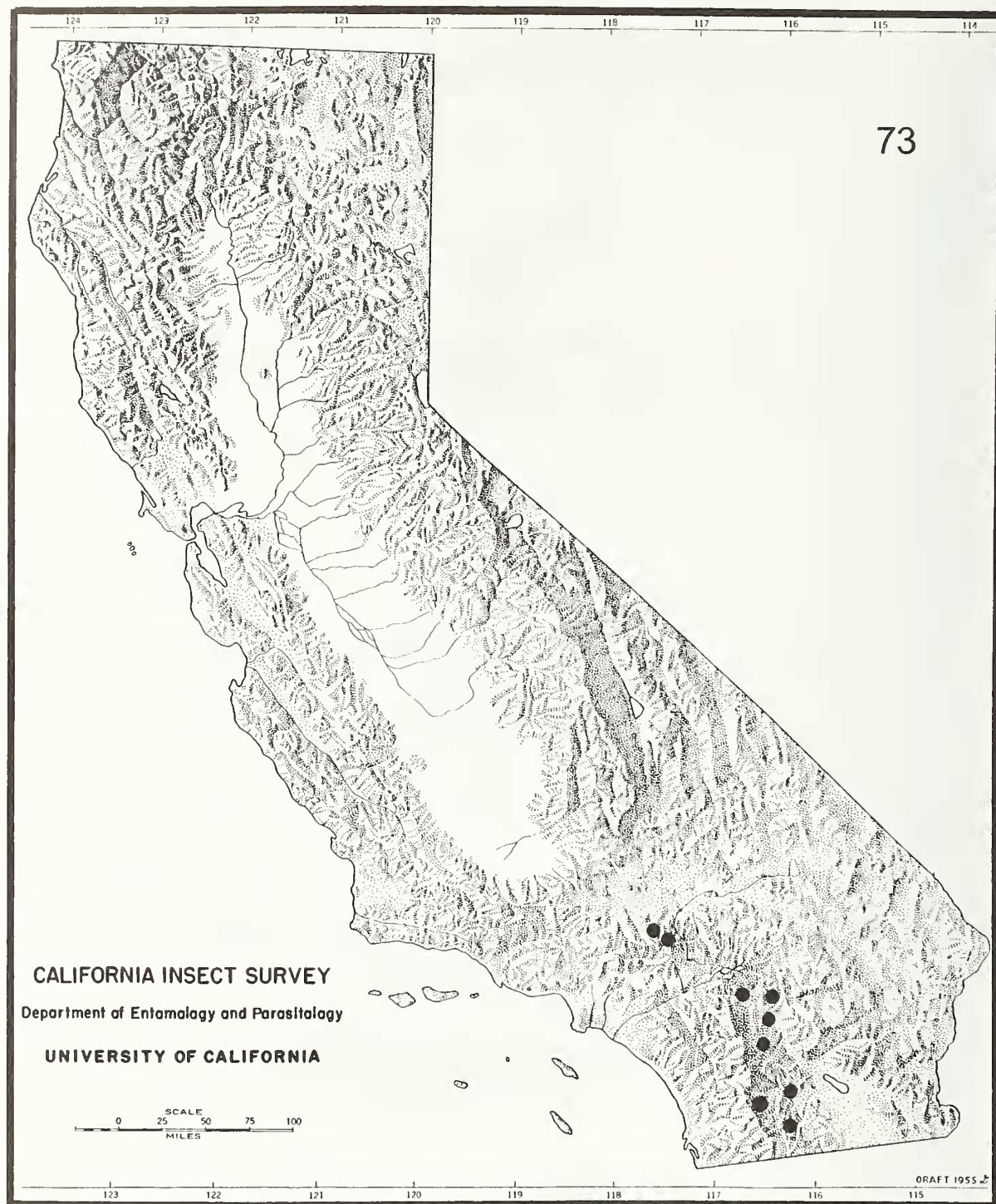
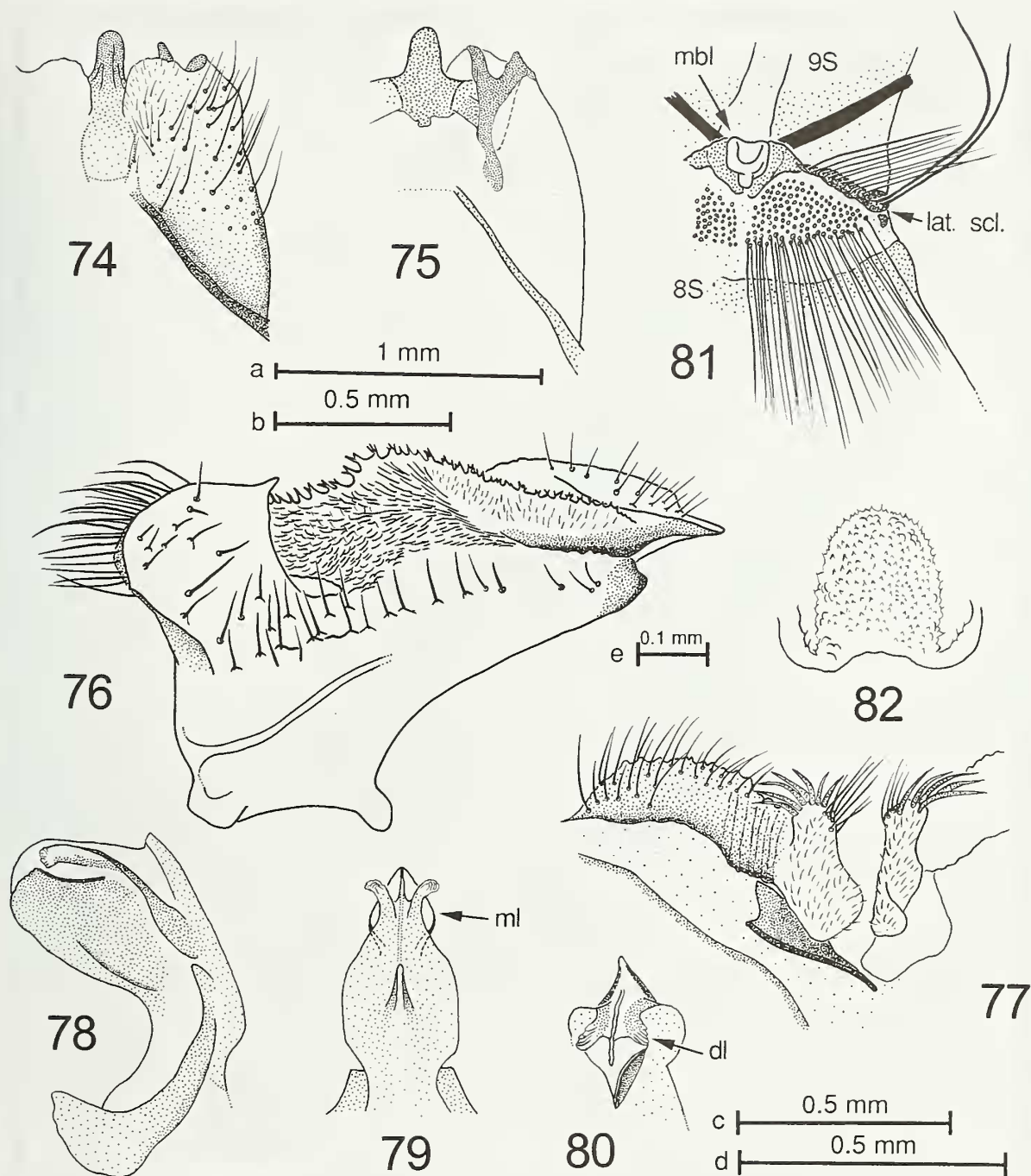


Fig. 73. Distribution of *Tipula* (*Eremotipula*) *melanderiana* Alexander.



Figs. 74-82. *Tipula (Eremotipula) larreae*, male. 74-75, ninth tergum, dorsal and ventral views. 76, inner dististyle, lateral view. 77, appendage of ninth sternum, posterolateral view. 78-80, adminiculum, lateral, dorsal and posterior views. 81, intersegmental area between eighth and ninth sterna. 82, membranous lobe. Scale a: 74-75, 81; b: 77; c: 78-80; d: 76; e: 82.

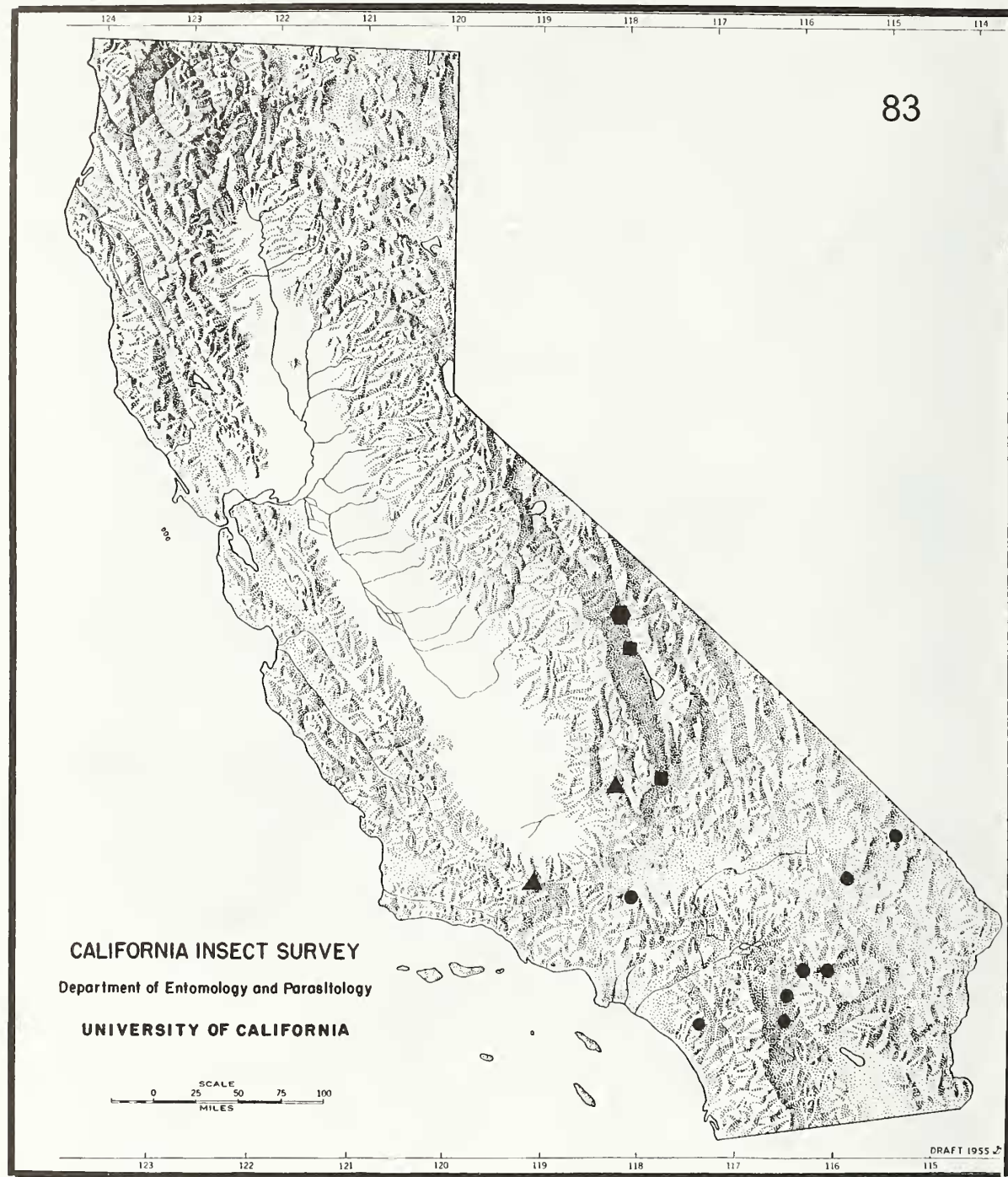
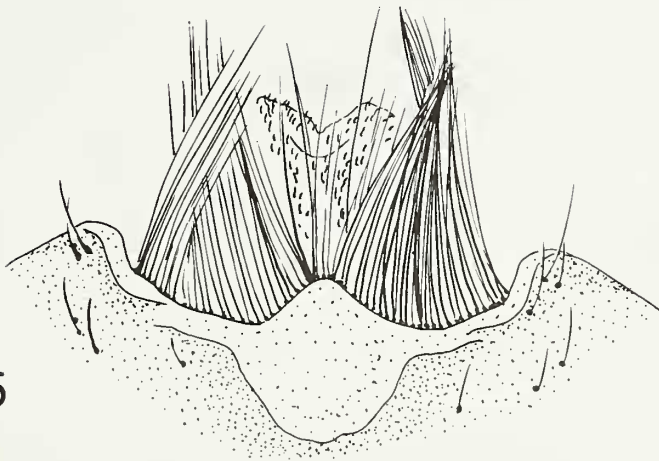


Fig. 83. Distribution of *Tipula* (*Eremotipula*) *baumanni* n. sp. (hexagon), *helpferi* Alexander (squares), *larreae*, n. sp. (circles) and *spinerecta* Alexander (triangles).

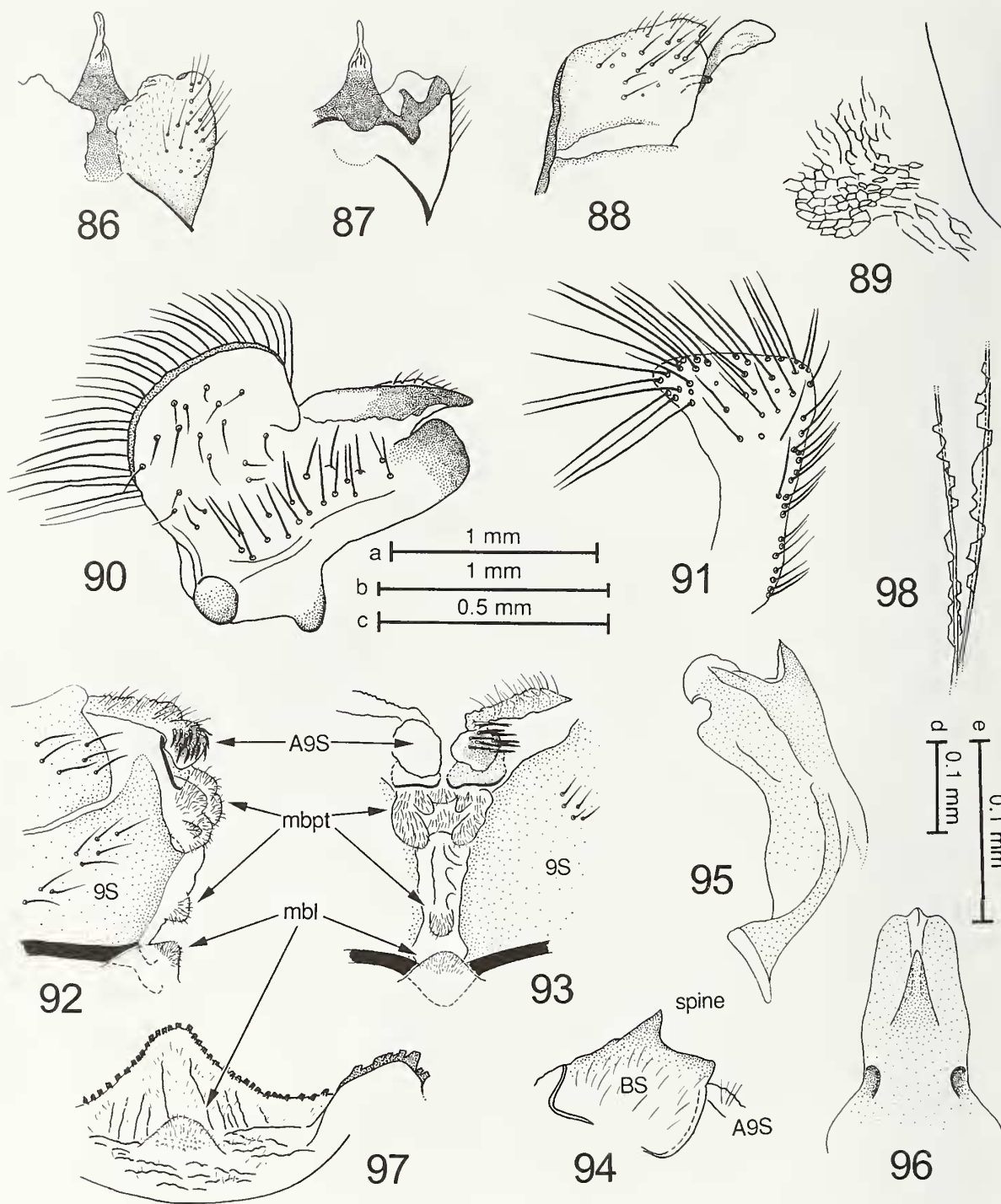


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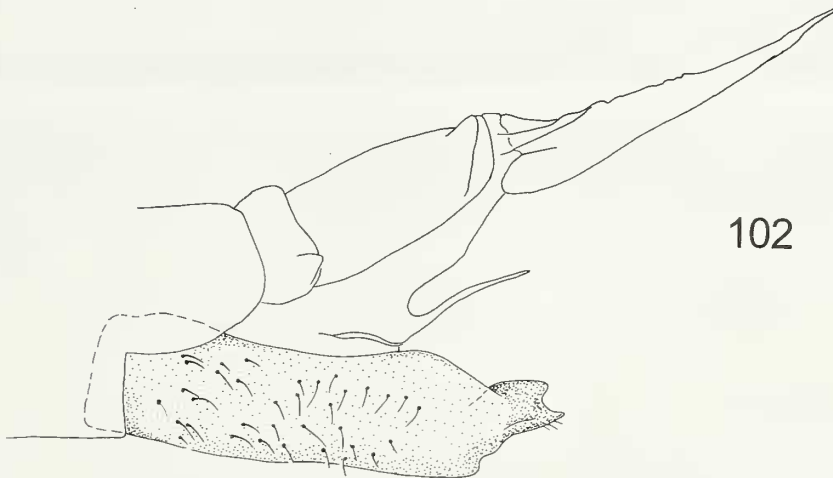
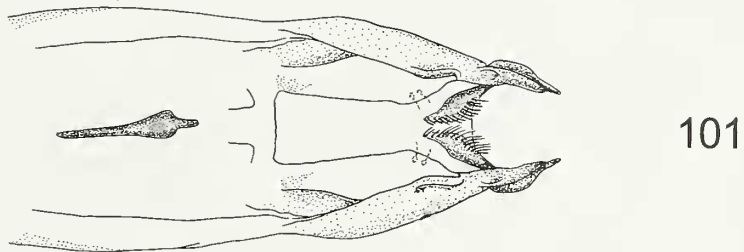
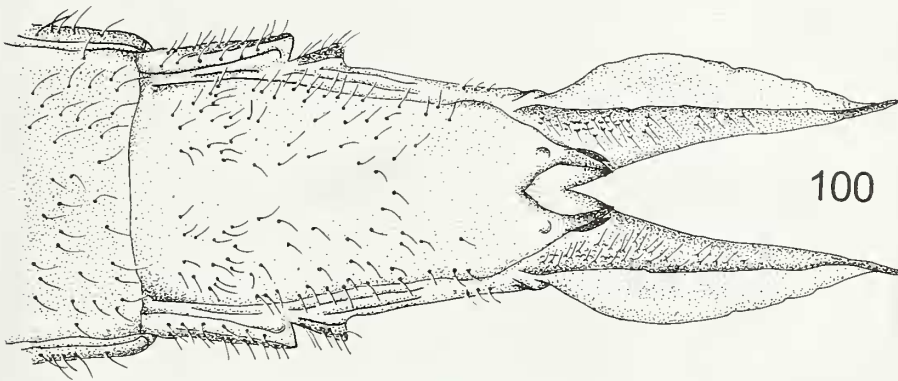
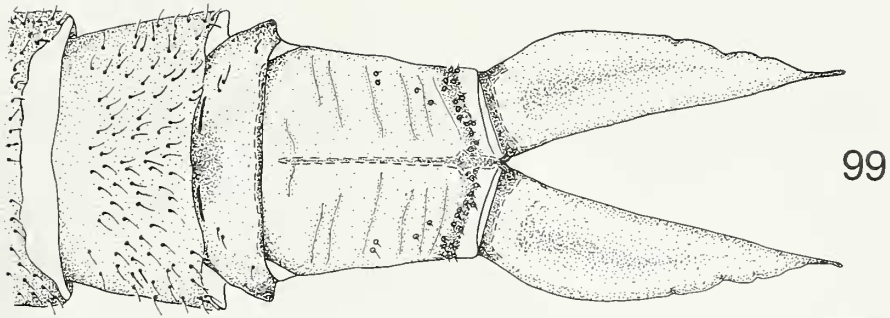


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Figs. 84–85. *Tipula* (*Eremotipula*) *curystyla*, male. 84, hypopygium, lateral view. 85, apex of eighth sternum and protuberance of ninth sternum.



Figs. 86-98. *Tipula* (*Eremotipula*) *eurystyla*, male. 86-88, ninth tergum, dorsal, ventral and lateral views. 89, detail of reticulate cuticle at base of subtergal process. 90, inner dististyle, lateral view. 91, outer dististyle, lateral view. 92-93, ninth sternum, lateral and posterior views. *mbl* = membranous lobe, *mbpt* = membranous protuberance. 94, spine on basistyle. 95-96, adminiculum, lateral and dorsal views. 97, apex of eighth sternum, inner view with only bases of setae shown. 98, detail of setae of eighth sternum. Scale a: 94; b: 86-88, 92-93; c: 90-91, 95-97; d: 98; e: 89.



Figs. 99–102. *Tipula* (*Eremotipula*) *eurystyla*, female genitalia. 99, dorsal view. 100, ventral view. 101, inner view of eighth sternum, hypogynial valves and vaginal apodeme. 102, lateral view.

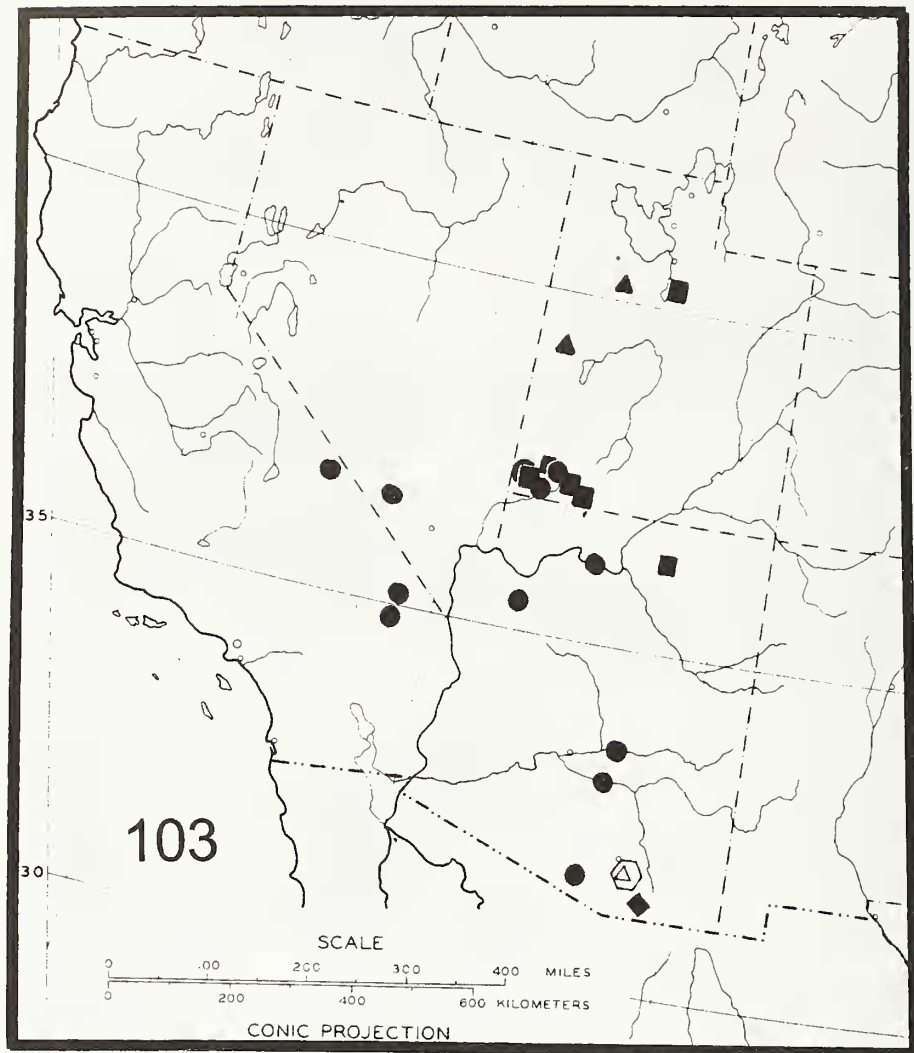
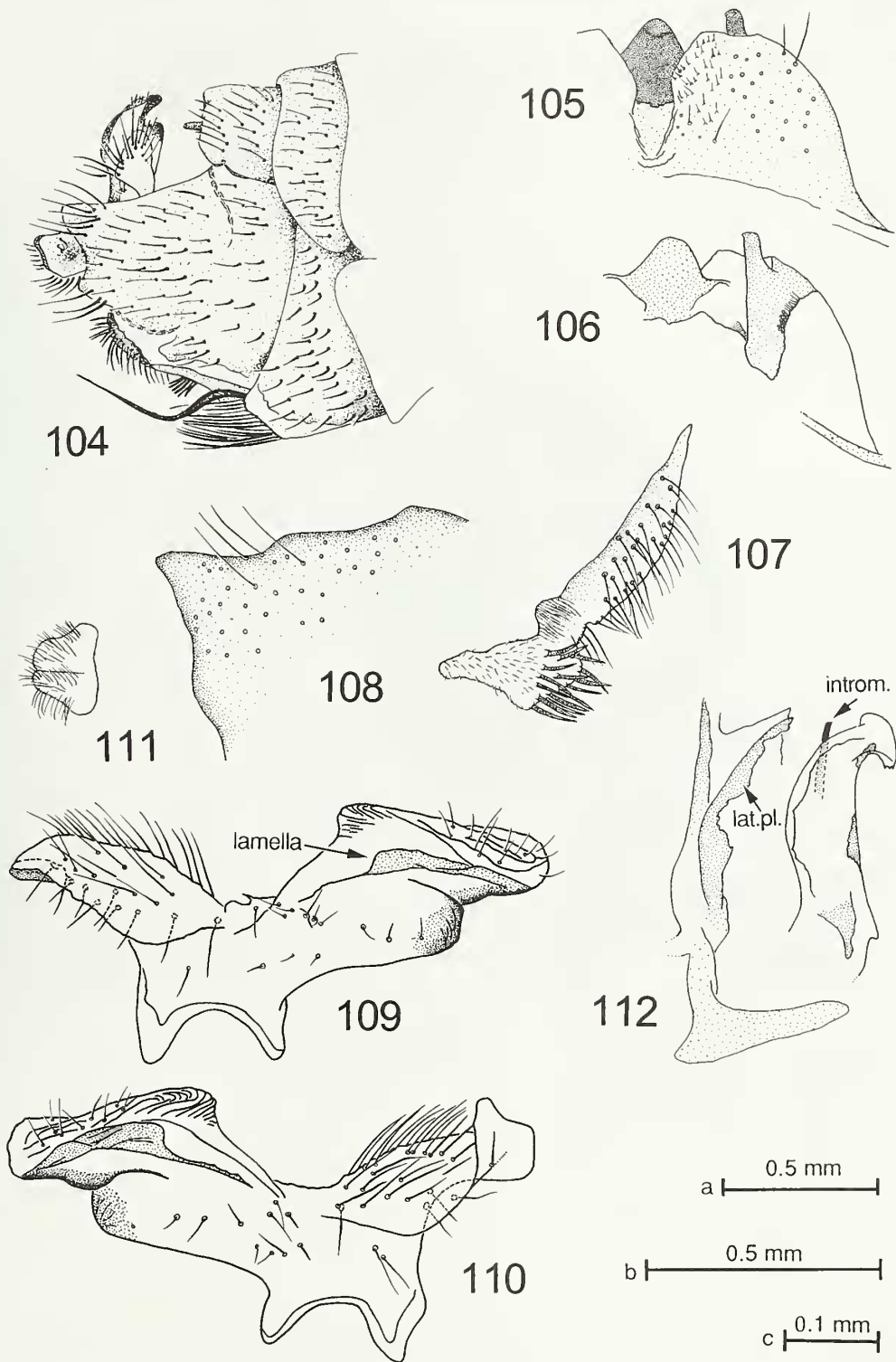


Fig. 103. Distributions of *Tipula* (*Eremotipula*) *eurystyla* Alexander (squares), *kirkwoodi* Alexander (hexagon), *macracantha* Alexander (circles), *maderensis* n. sp. (open triangle), *rogersi* n. sp. (diamond) and *utahicola* Alexander (triangle).



Figs. 104–112. *Tipula (Eremotipula) utahicola*, male. 105–106, ninth tergum, dorsal and ventral views. 107, appendage of ninth sternum, lateral view. 108, spine of basistyle. 109–110, inner dististyle, lateral view (both left and right dististyles shown). 111, membranous protuberance of ninth sternum. 112, adminiculum, lateral view (broken on slide). *introm.* = intromittent organ, *lat. pl.* = lateral plate. Scale a: 105–106, 108; b: 107, 109–110, 112; c: 111.

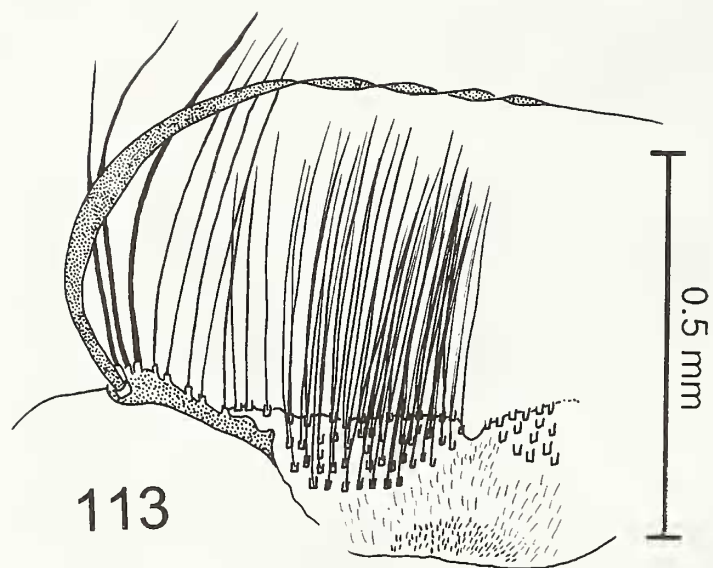
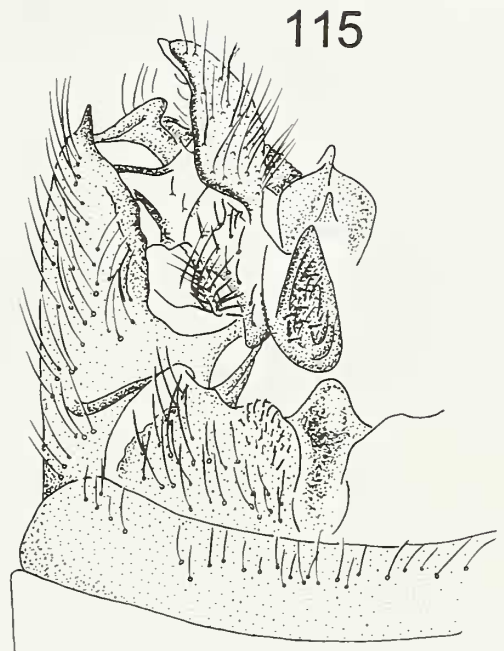
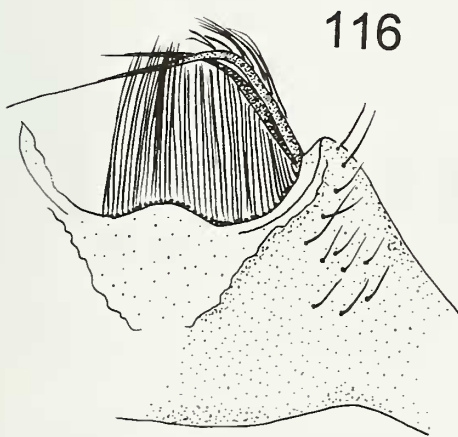
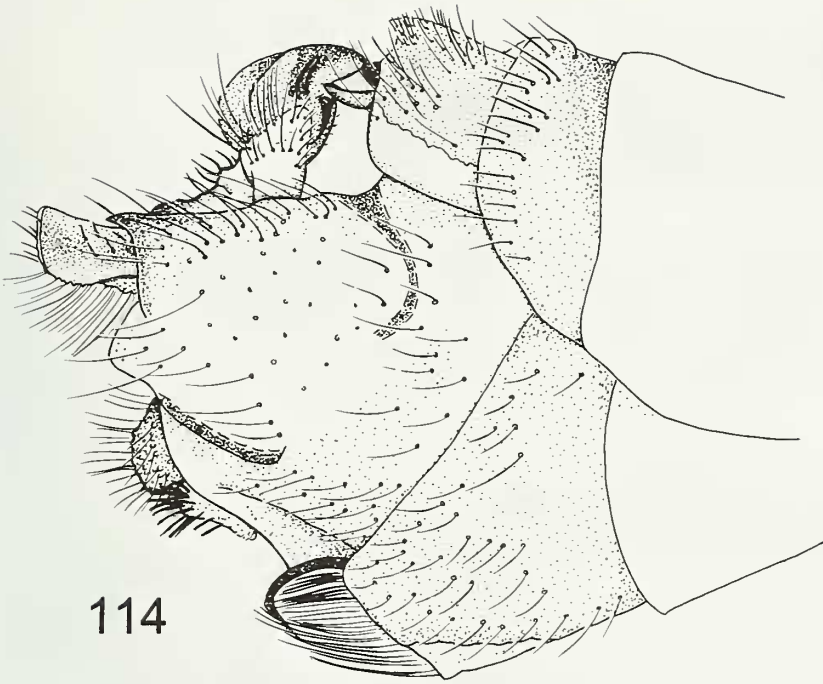
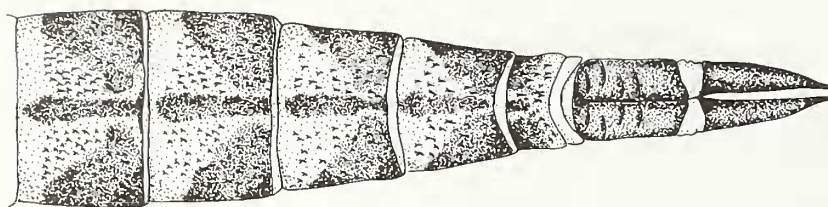


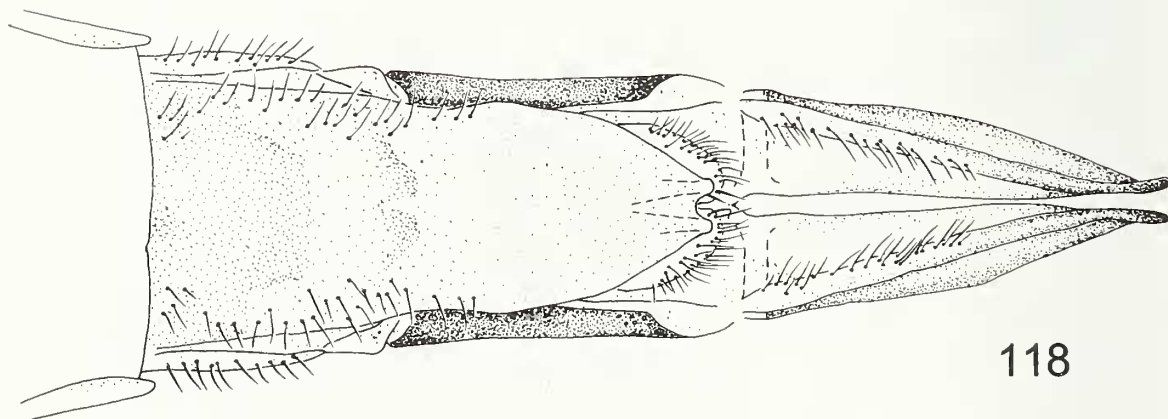
Fig. 113. *Tipula* (*Eremotipula*) *utahicola*, male eighth sternum (one half detailed only).



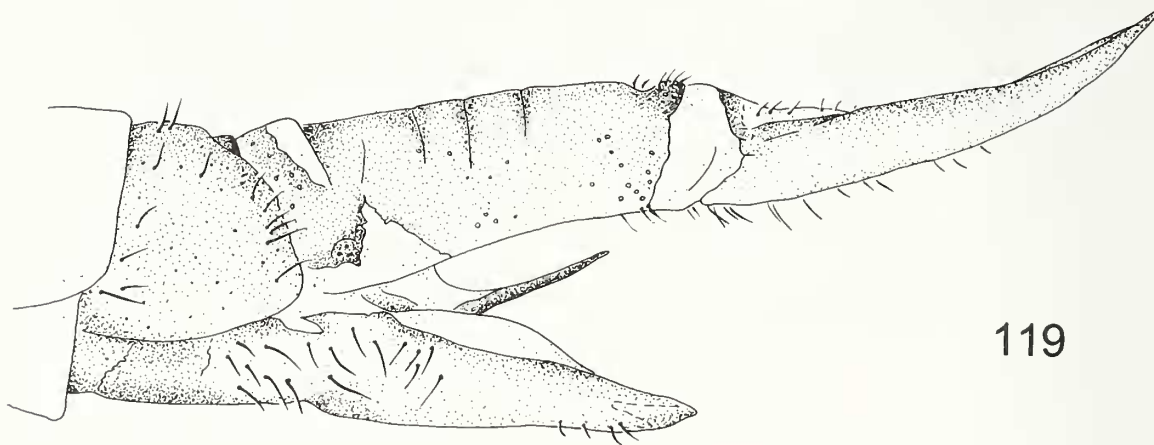
Figs. 114–116. *Tipula (Eremotipula) baumanni*, n. sp., male. 114, hypopygium, lateral view. 115, hypopygium, dorsal view (right side shown). 116, apex of eighth sternum.



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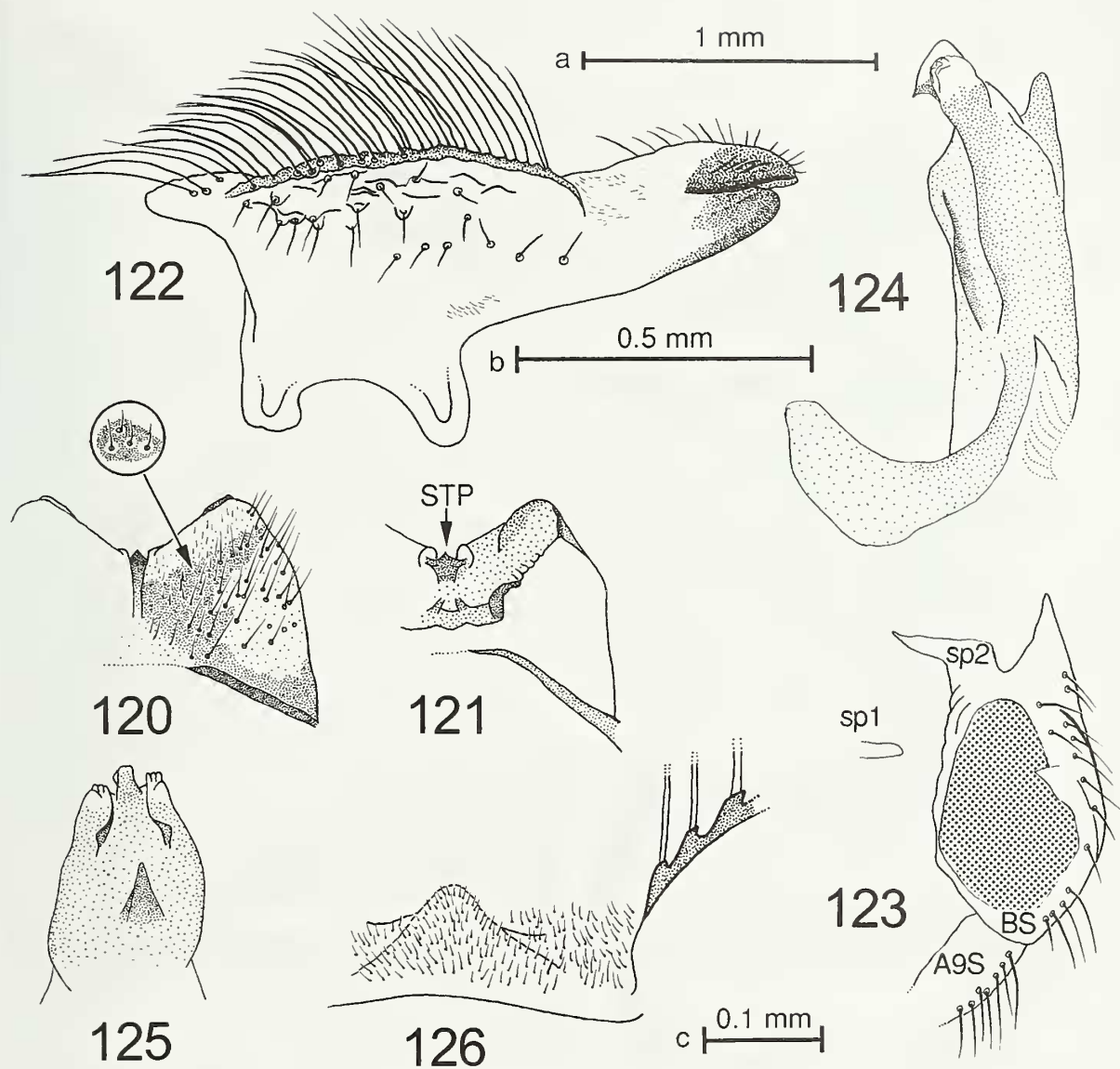


118

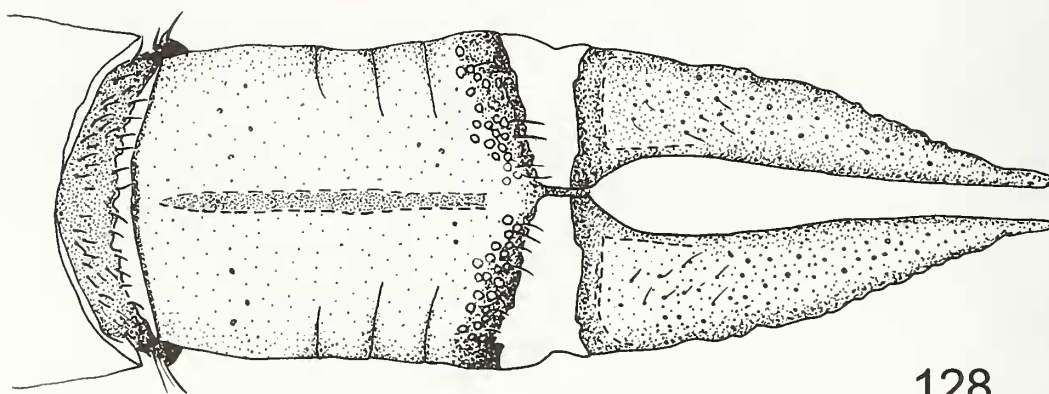
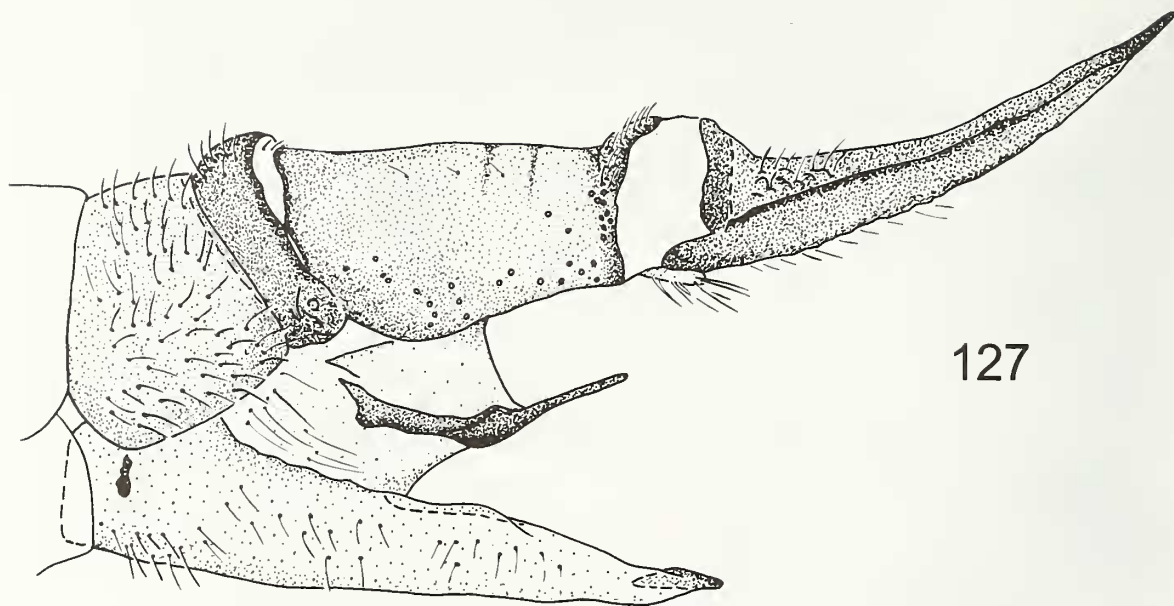


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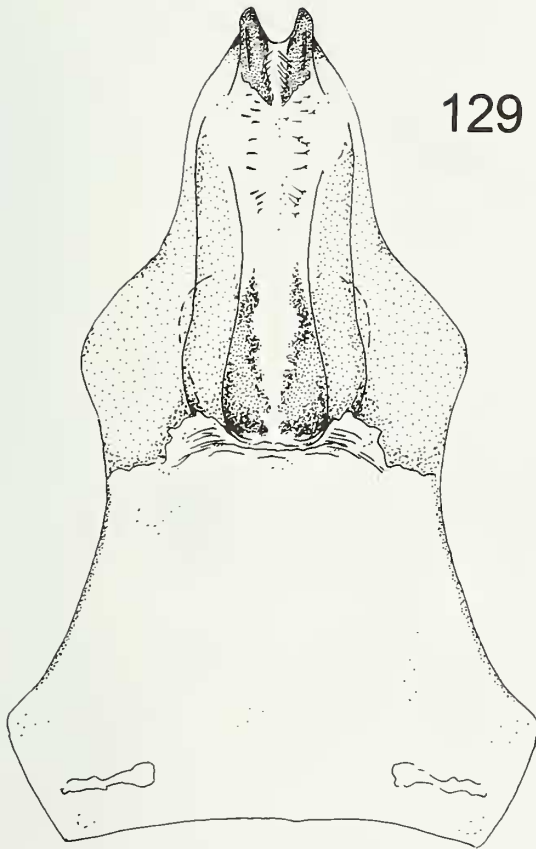
Figs. 117–119. *Tipula* (*Eremotipula*) *elverae*, n. sp. female. 117, abdomen, dorsal view. 118, genitalic segments, ventral view. 119, genitalic segments, lateral view.



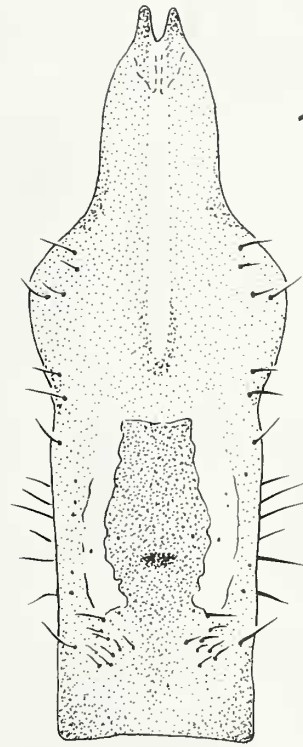
Figs. 120–126. *Tipula* (*Eremotipula*) *helferi*, male. 120–121, ninth tergum, dorsal and ventral view, inset of short, pale, dorsal setae. 122, inner dististyle, lateral view. 123, basistyle, dorsal view (dististyles removed). 124–125, adminiculum, lateral and dorsal views. 126, membranous lobe of eighth sternum, inner view. Scale a: 120–121, 123; b: 122, 124–125; c: 126.



Figs. 127–128. *Tipula* (*Eremotipula*) *helferi*, female genitalia. 127, lateral view. 128, dorsal view.

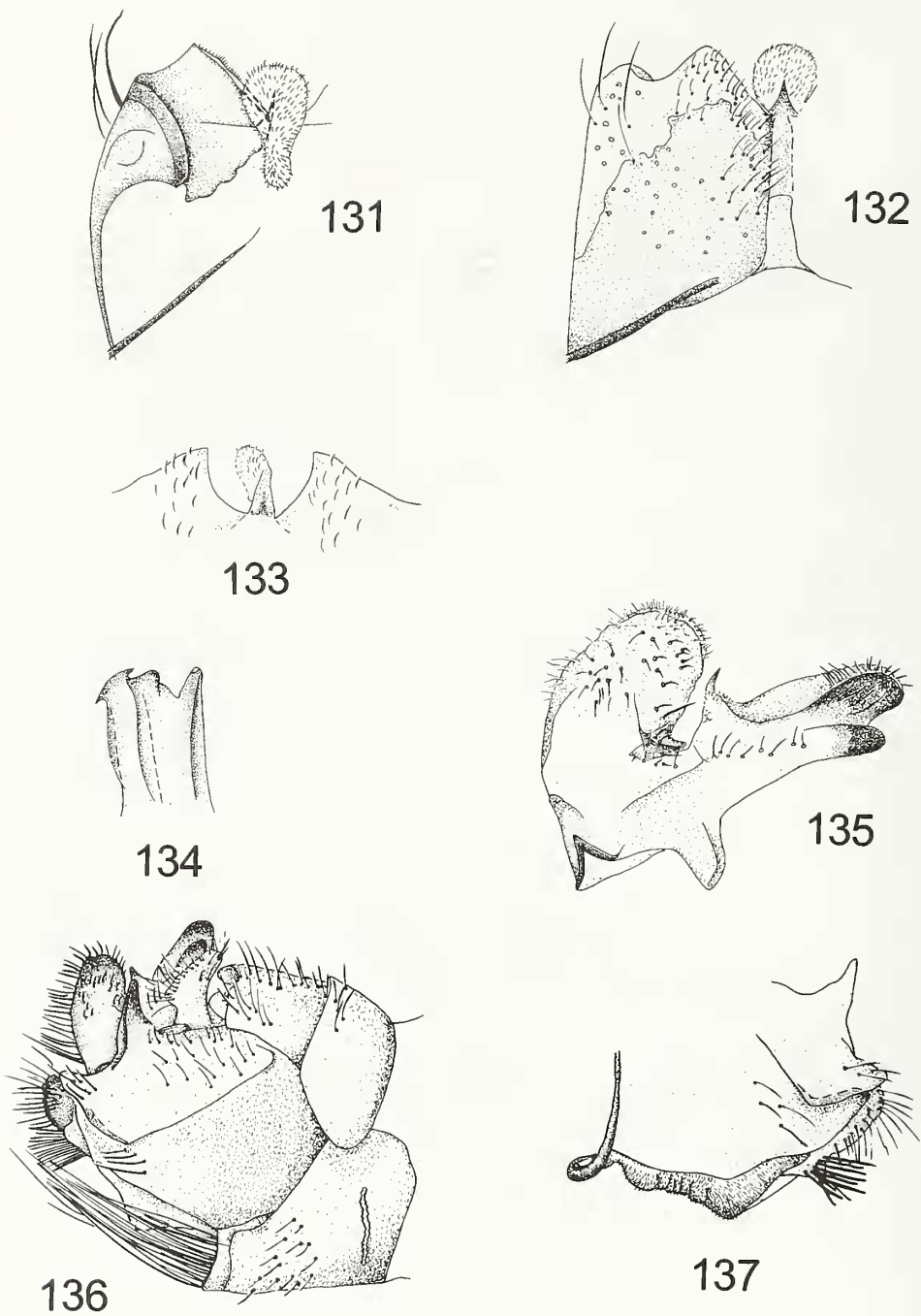


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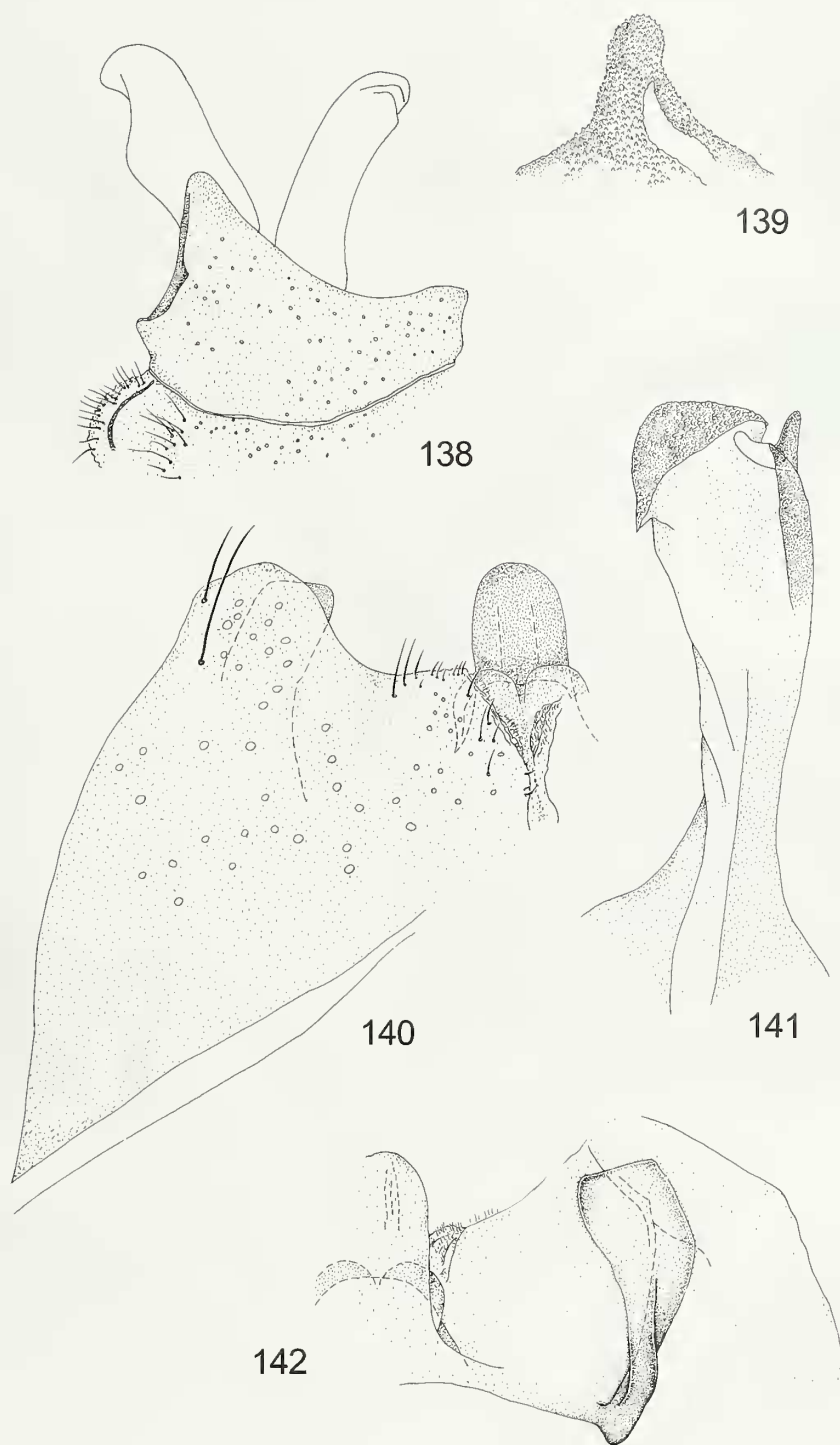


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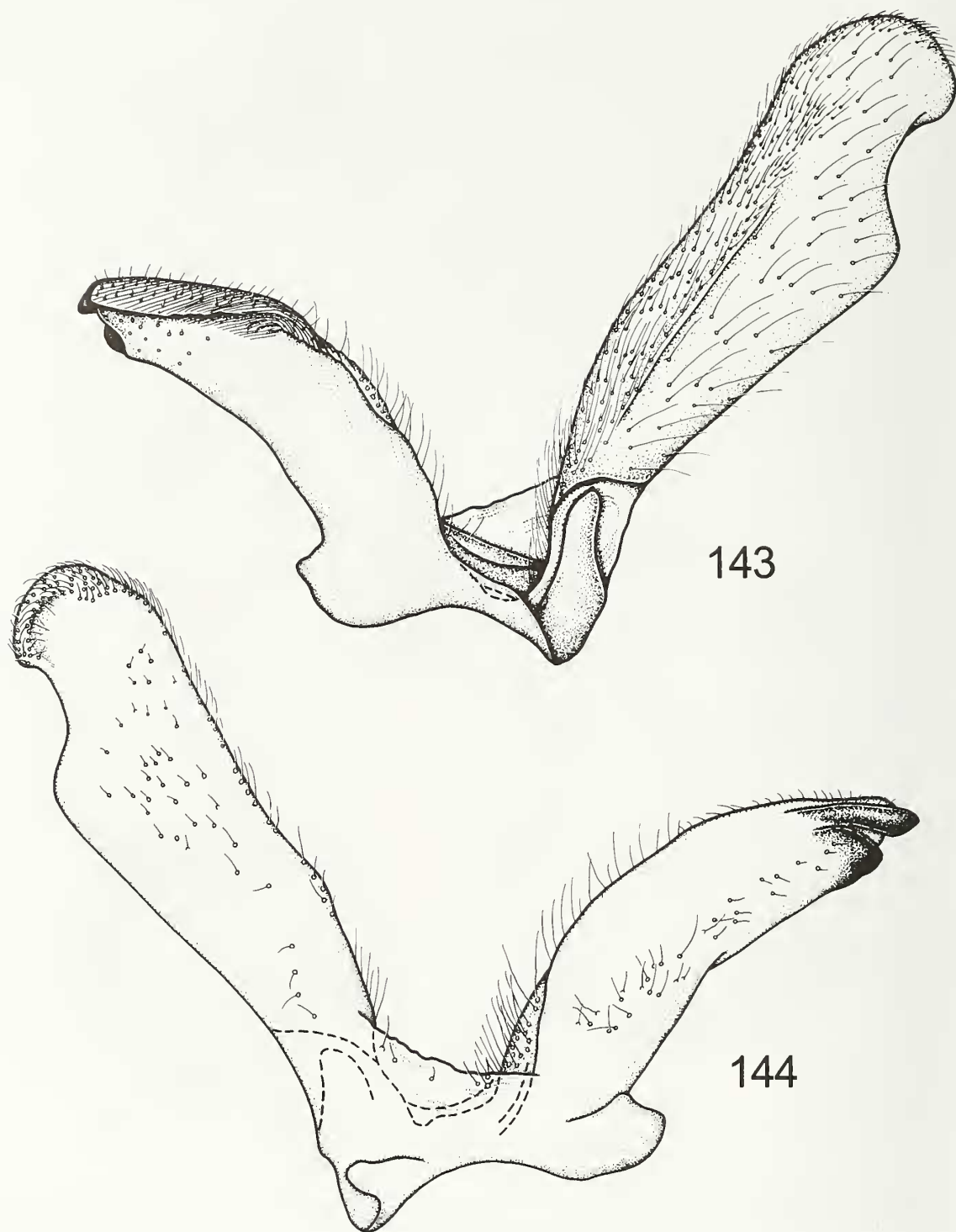
Figs. 129–130. *Tipula (Eremotipula) helferi*, female eighth sternum and hypogynial valves. 129, inner view. 130, ventral view.



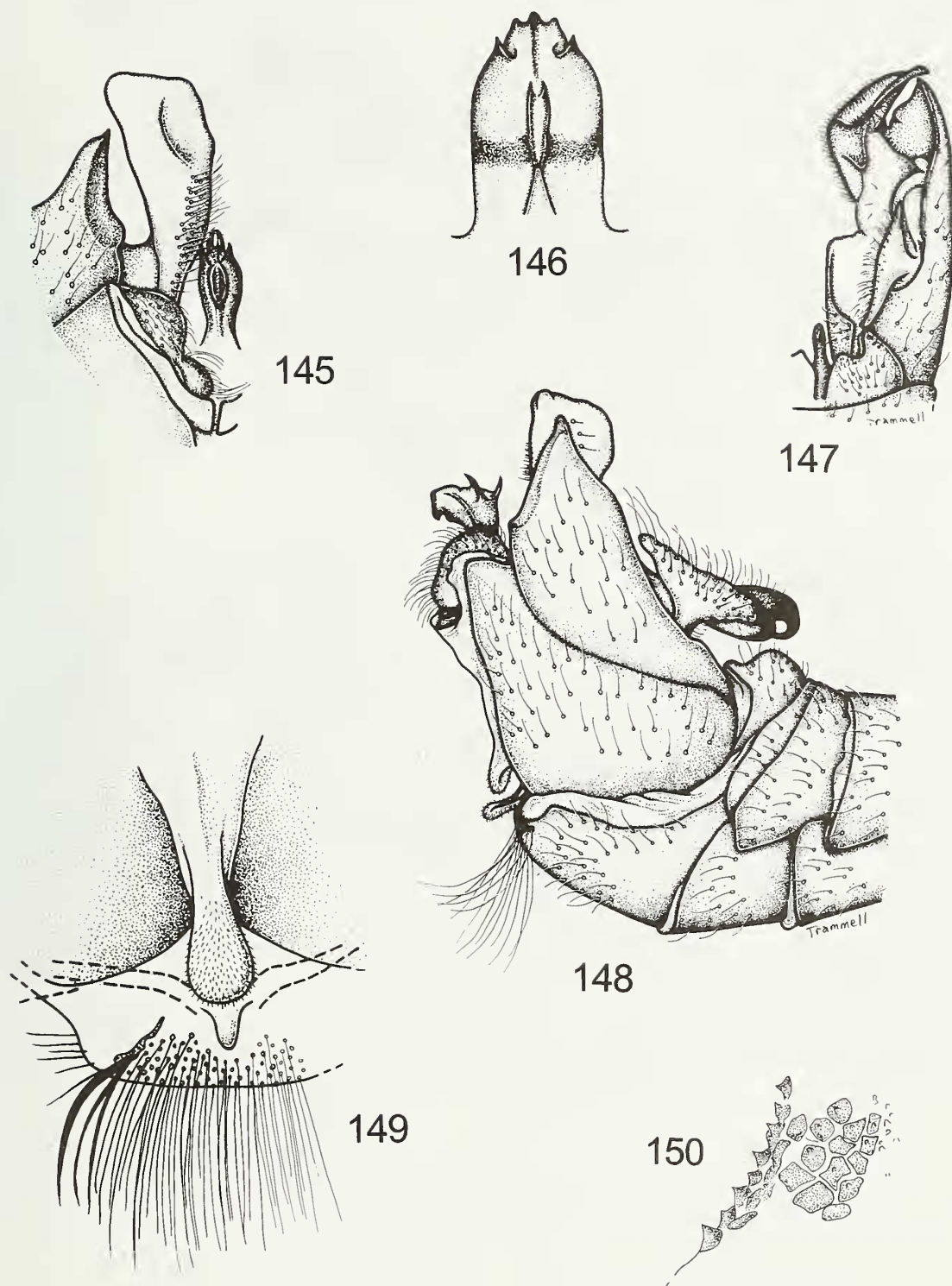
Figs. 131–137. *Tipula (Eremotipula) spinerecta* Alexander, male. 131–132, ninth tergum, ventral and dorsal view. 133, ninth tergum, median area, from slide mount. 134, adminiculum, lateral view. 135, inner dististyle, lateral view. 136, hypopygium, lateral view. 137, basistyle and ninth sternum, lateral view.



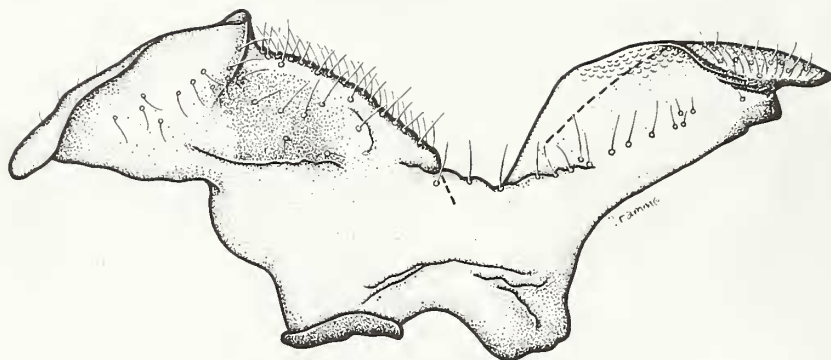
Figs. 138–142. *Tipula (Eremotipula) kirkwoodi* Alexander, male. Drawn from slide mounts. 138, basistyle and ninth sternum, lateral view. 139, membranous lobe of the eighth sternum. 140, 142, ninth tergum, dorsal and ventral view. 141, adminiculum, posterolateral view.



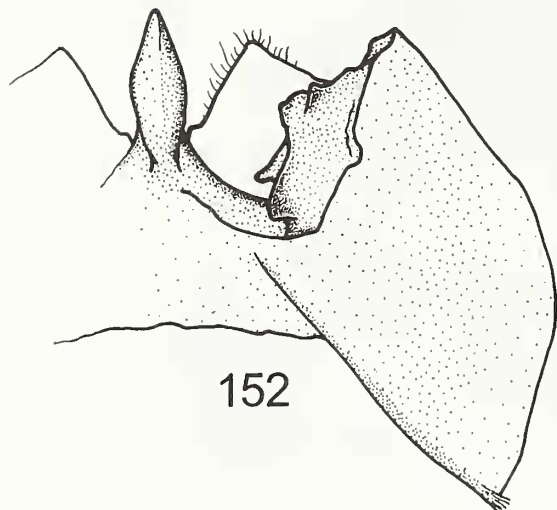
Figs. 143–144. *Tipula* (*Eremotipula*) *kirkwoodi* Alexander, male. Drawn from slide mounts. 143, inner dististyle, mesal view. 144, inner dististyle, lateral view.



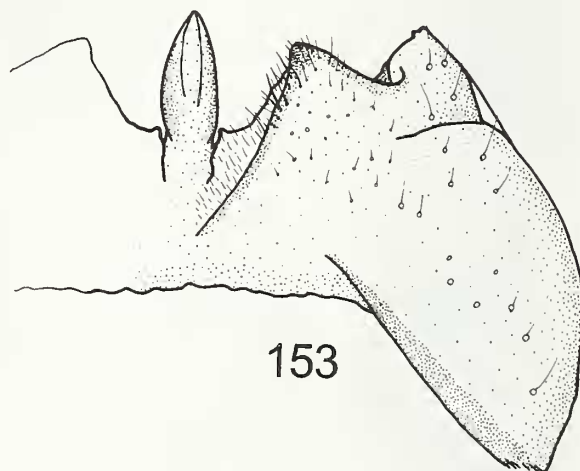
Figs. 145–150. *Tipula (Eremotipula) rogersi* n. sp., male. 145, hypopygium, posterior view. 146, adminiculum, dorsal view. 147, hypopygium, dorsal view. 148, hypopygium, lateral view. 149, membranous protuberance of 9S and apex of eighth sternum. 150, spinules of membranous lobe of 8S.



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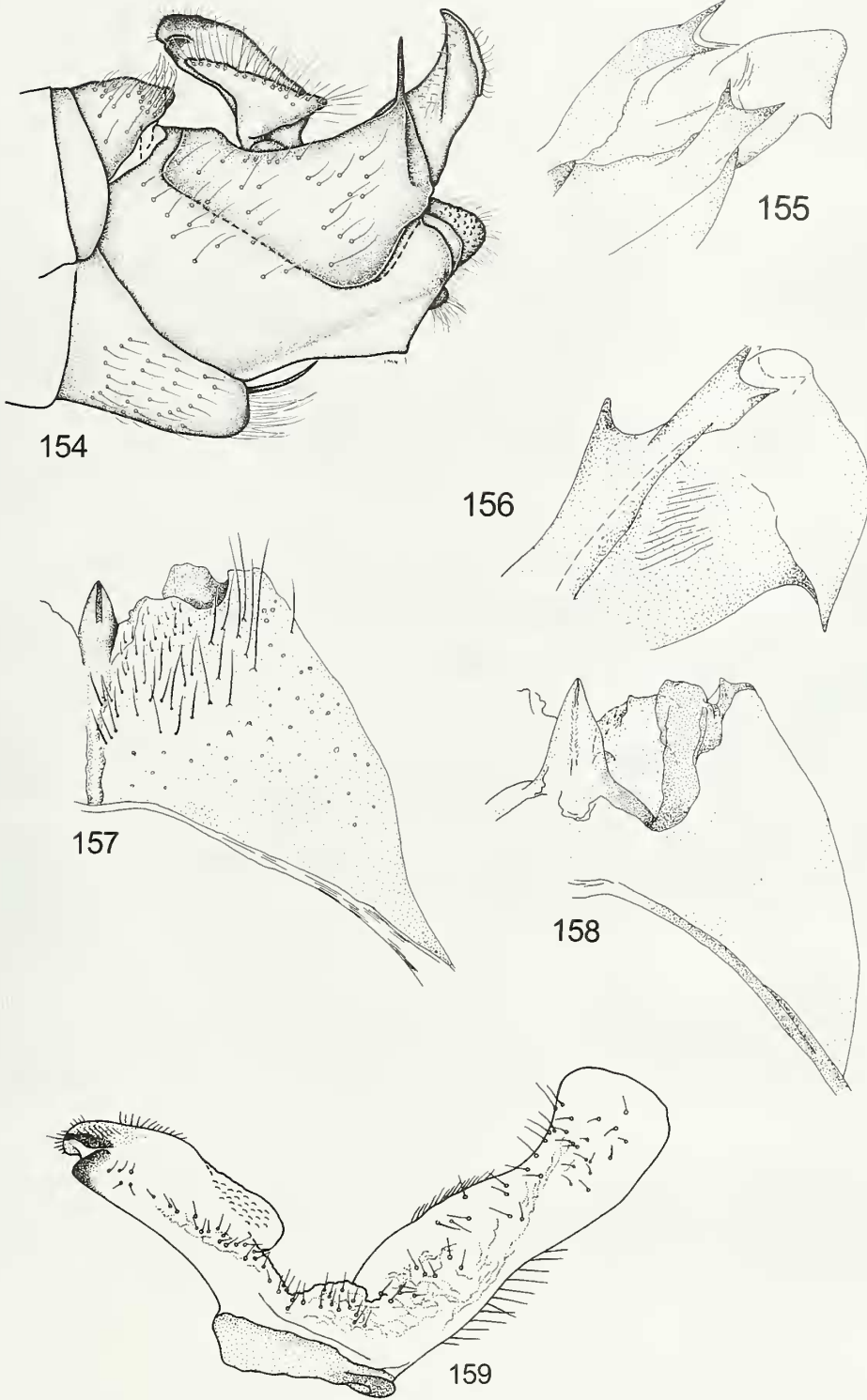


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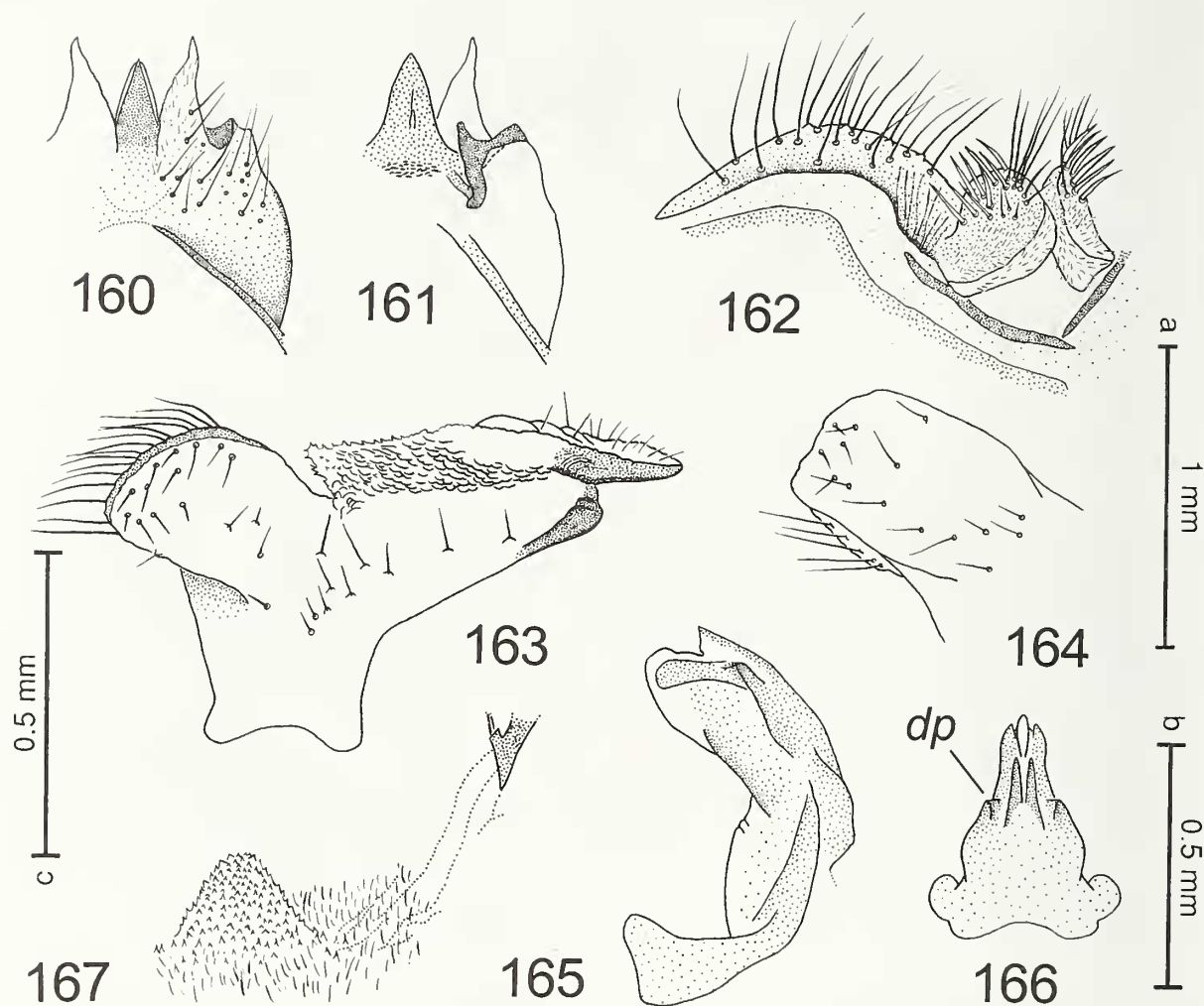


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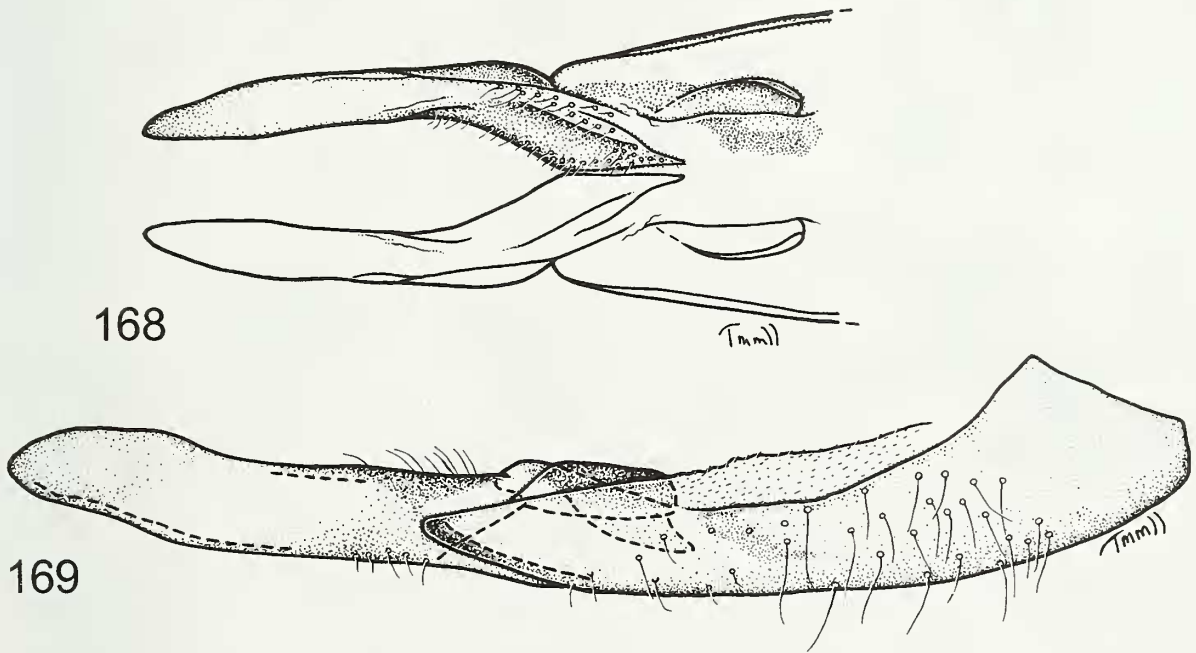
Figs. 151–153. *Tipula* (*Eremotipula*) *rogersi* n. sp., male. 151, inner dististyle, lateral view. 152, 153, ninth tergum, ventral and dorsal view.



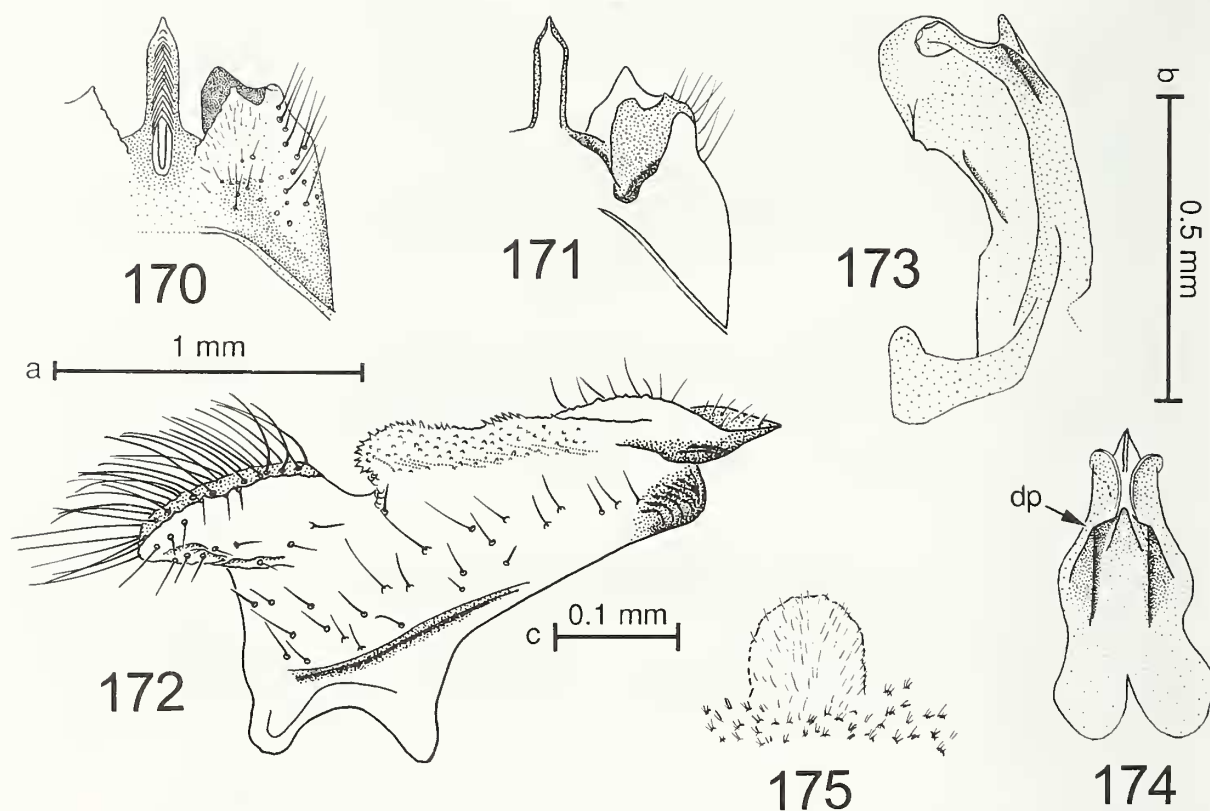
Figs. 154–159. *Tipula* (*Eremotipula*) *maderensis* n. sp., male. 154, hypopygium, lateral view. 155–156, adminiculum, dorsoposterior and lateral views. 157–158, ninth tergum, dorsal and ventral views. 159, inner dististyle, lateral view.



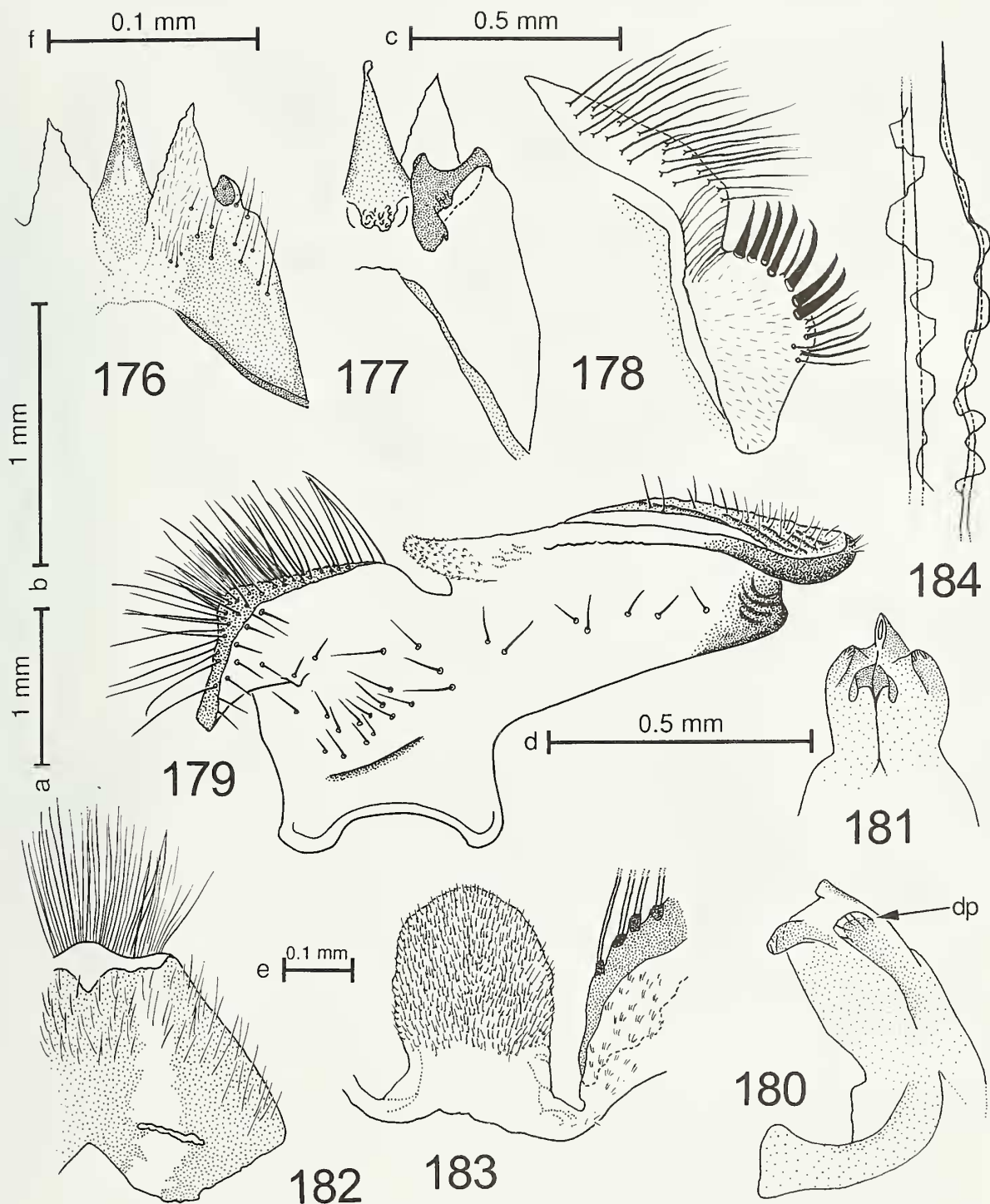
Figs. 160–167. *Tipula* (*Eremotipula*) *macracantha*, male. 160, 161, ninth tergum, dorsal and lateral views. 162, appendage of ninth sternum, lateral view (part of opposing lobe shown). 163, inner dististyle, lateral view. 164, outer basal lobe of inner dististyle, lateral view, holotype. 165, 166, adminiculum, lateral and dorsal views. *dp* = dorsal process. 167, membranous lobe of eighth sternum, inner view. Scale a: 160–161; b: 162; c: 163–167.



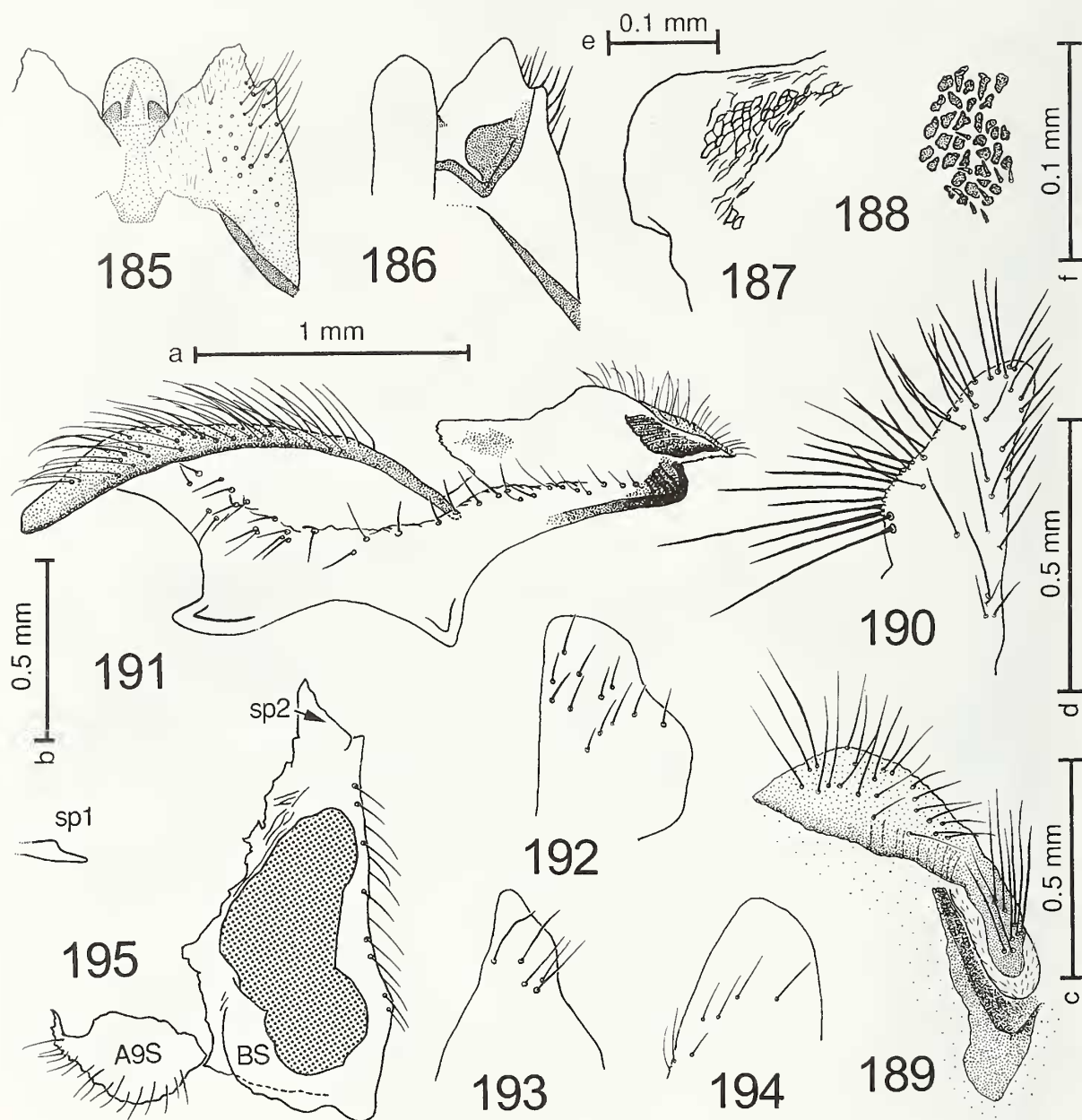
Figs. 168–169. *Tipula* (*Eremotipula*) *macracantha*, female, eighth sternum and hypogynial valves. 168, inner view. 169, lateral view.



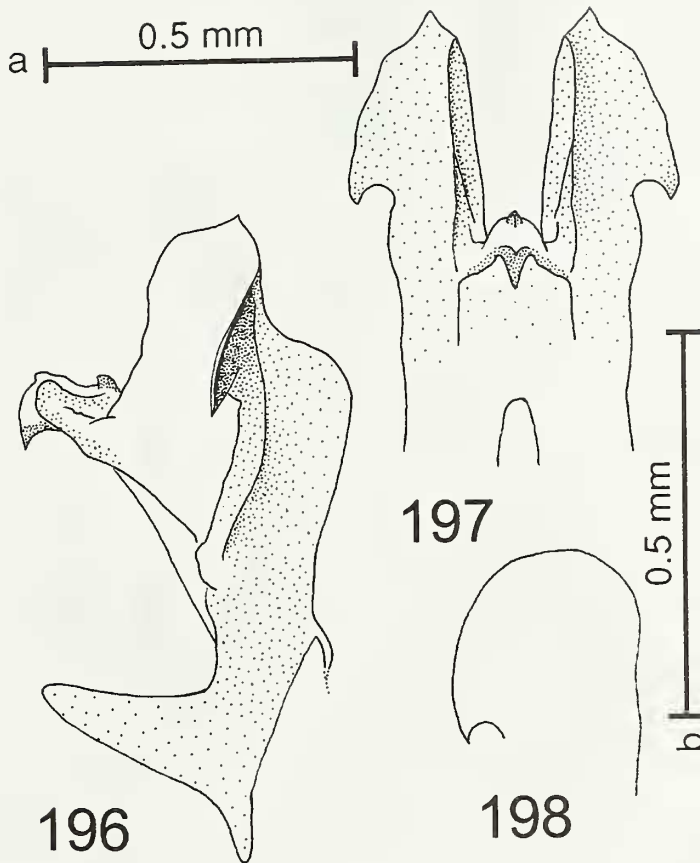
Figs. 170–175. *Tipula (Eremotipula) artemisiae*, male. 170, 171, ninth tergum, dorsal and ventral views. 172, inner dististyle, lateral view. 173, 174, adminiculum, lateral and dorsal views. *dp* = dorsal process. 175, membranous lobe of eighth sternum. Scale a: 170–171; b: 172–174; c: 175.



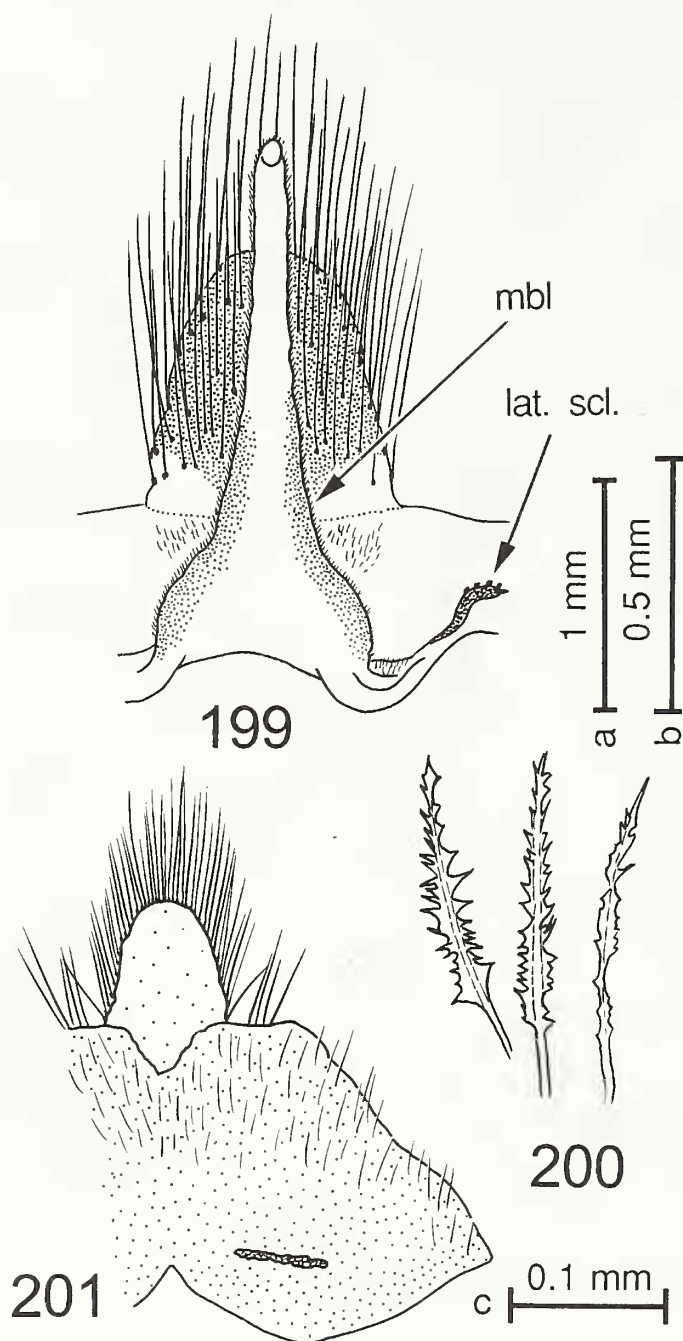
Figs. 176–184. *Tipula (Eremotipula) schusteri*, male. 176, 177, ninth tergum, dorsal and ventral views. 178, appendage of ninth sternum, lateral view. 179, inner dististyle, lateral view. 180, 181, adminiculum, lateral and posterior views. *dp* = dorsal process. 182, eighth sternum. 183, membranous lobe of eighth sternum, inner view. 184, carinate setae of eighth sternum. Scale a: 182; b: 176–177; c: 178; d: 179–181; e: 183; f: 184.



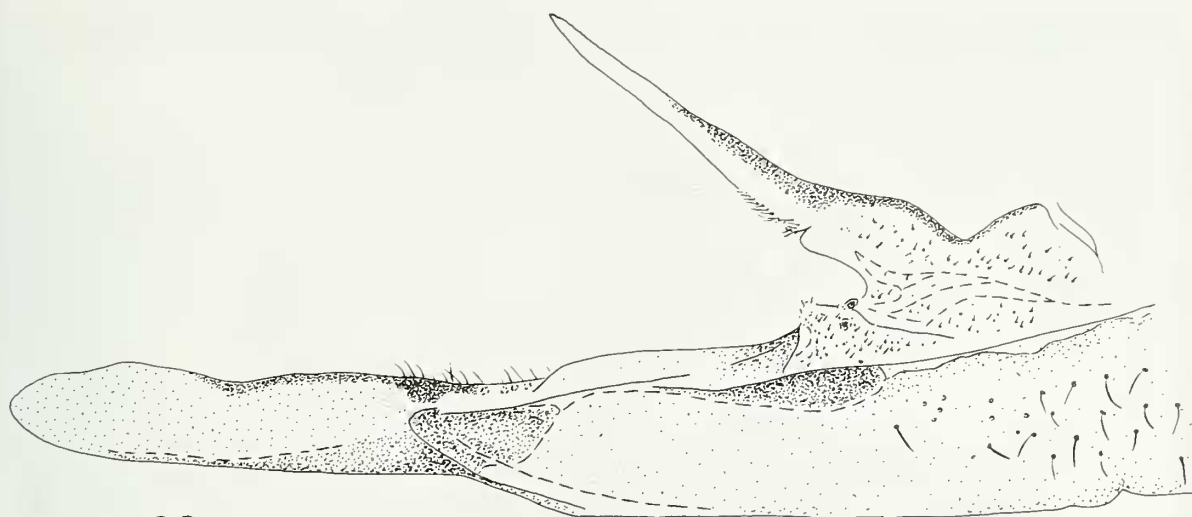
Figs. 185–195. *Tipula* (*Eremotipula*) *pellucida*. 185, 186, ninth tergum, dorsal and ventral views. 187, detail of cuticle of ventral lobe of ninth tergum. 188, detail of subtergal process of ninth tergum. 189, appendage of ninth sternum, posterodorsal view. 190, outer dististyle, lateral view. 191, inner dististyle, lateral view. 192–194, apex of outer basal lobe of inner dististyle, mesal view; 192 = Ravalli Co., Montana, 193 = Oneida Co., Idaho, 194 = Wenatchee, Washington. 195, basistyle, dorsal view (dististyles removed). Scale a: 185–186, 195; b: 177–180; c: 189; d: 190; e: 187; f: 188.



Figs. 196–198. *Tipula (Eremotipula) pellucida*, male. 196, 197, adminiculum, lateral and posterior views. 198, apex of dorsal process of adminiculum, Montana. Scale a: 196–197; b: 198.



Figs. 199–201. *Tipula* (*Eremotipula*) *pellucida*, male. 199, membranous lobe of eighth sternum, inner view. *lat. scl.* = lateral sclerite, *mbl* = membranous lobe. 200, carinate setae of eighth sternum. 201, eighth sternum. Scale a: 201; b: 199; c: 200.

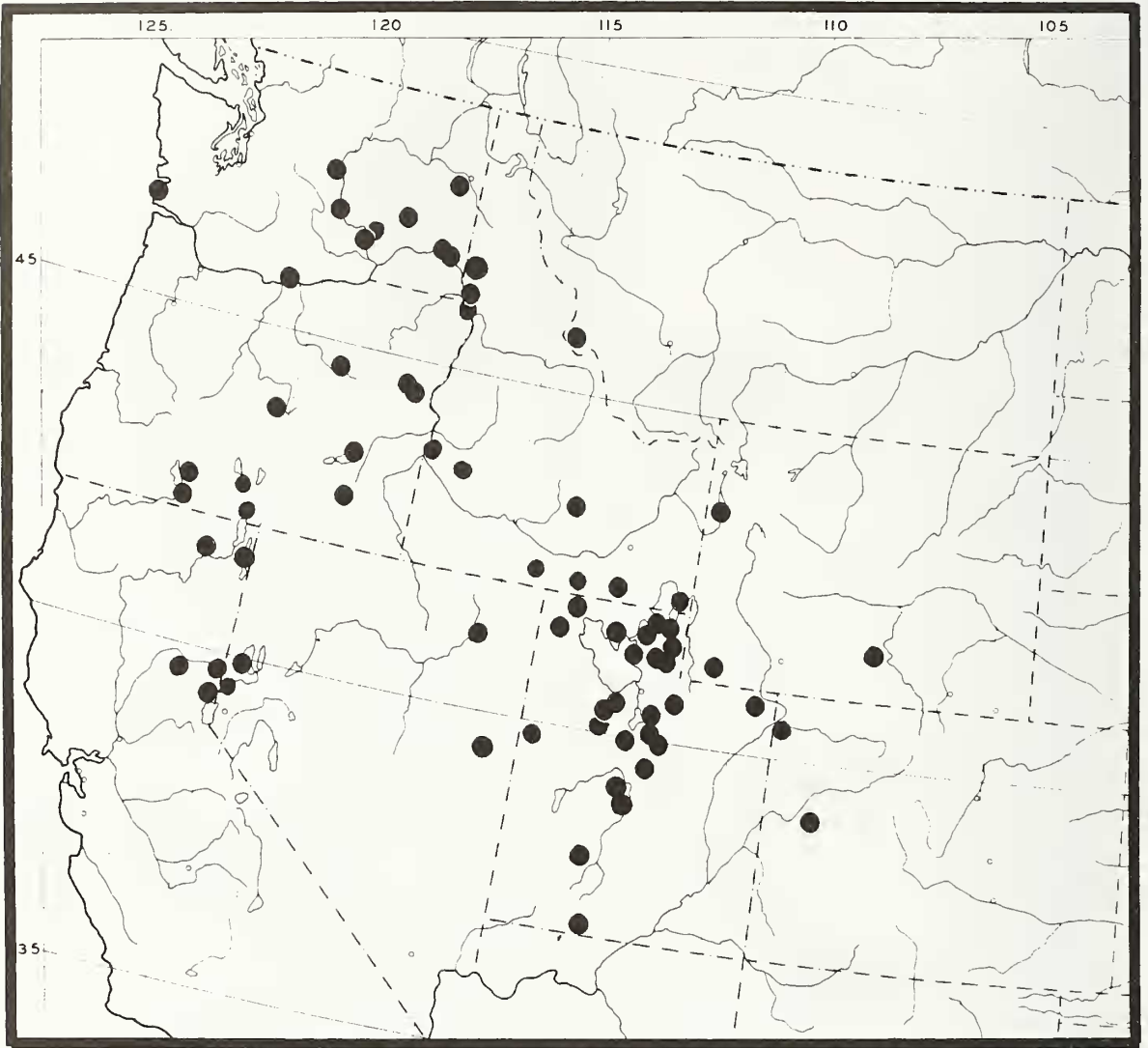


202



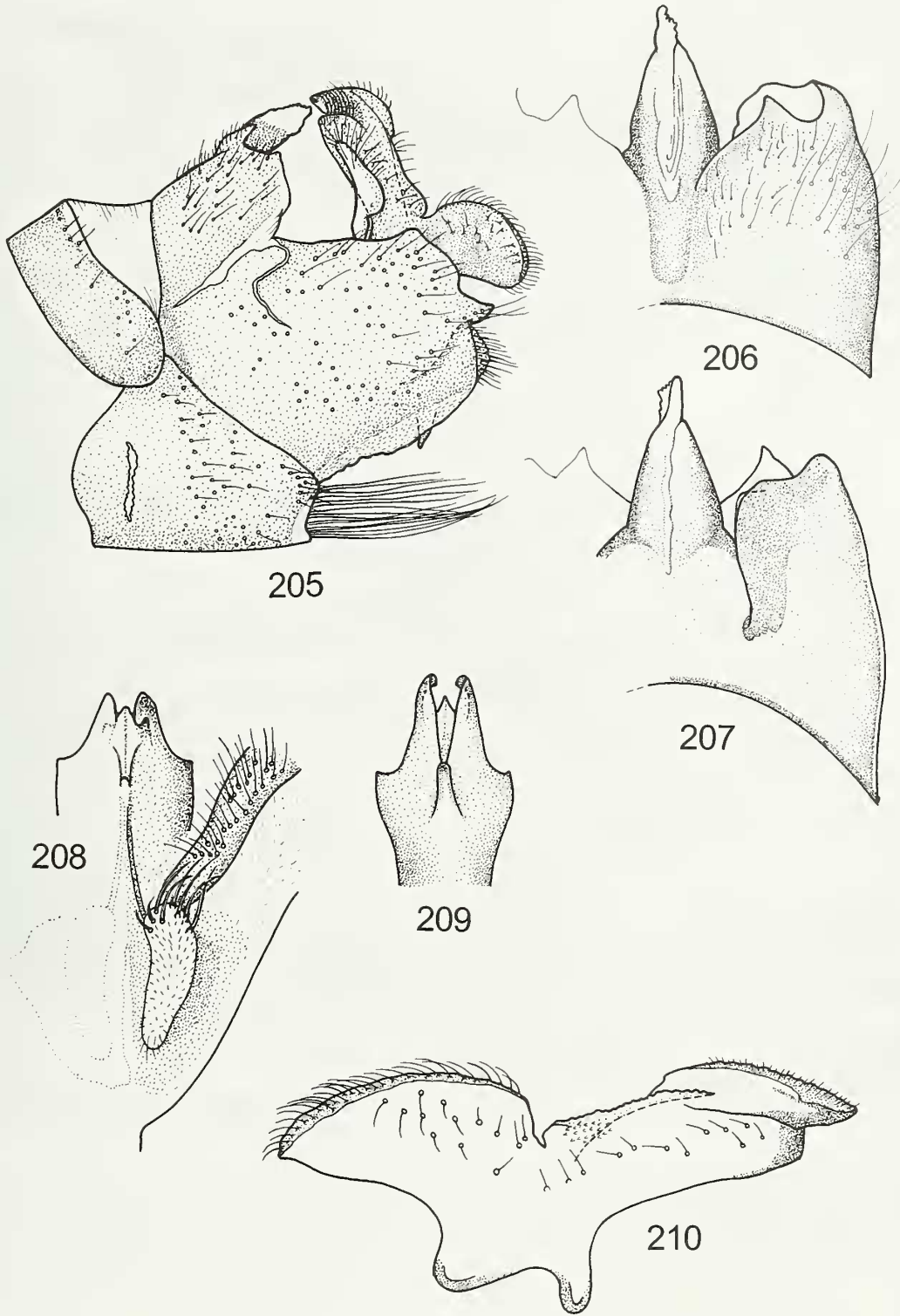
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Figs. 202–203. *Tipula* (*Eremotipula*) *pellucida*, female, eighth sternum and hypogynial valves. 202, lateral view, also showing fused valvulae. 203, inner view, also showing vaginal apodeme.

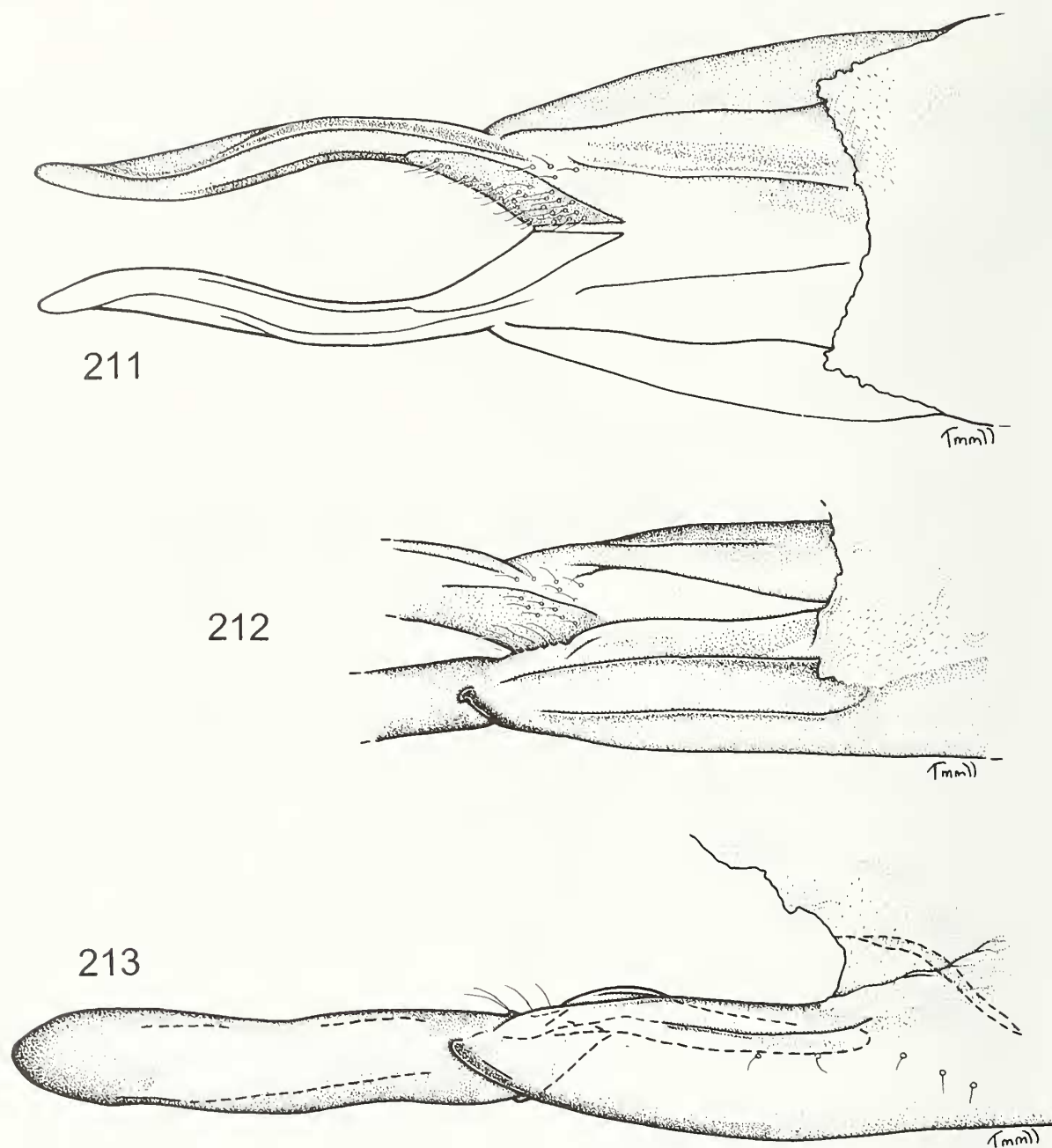


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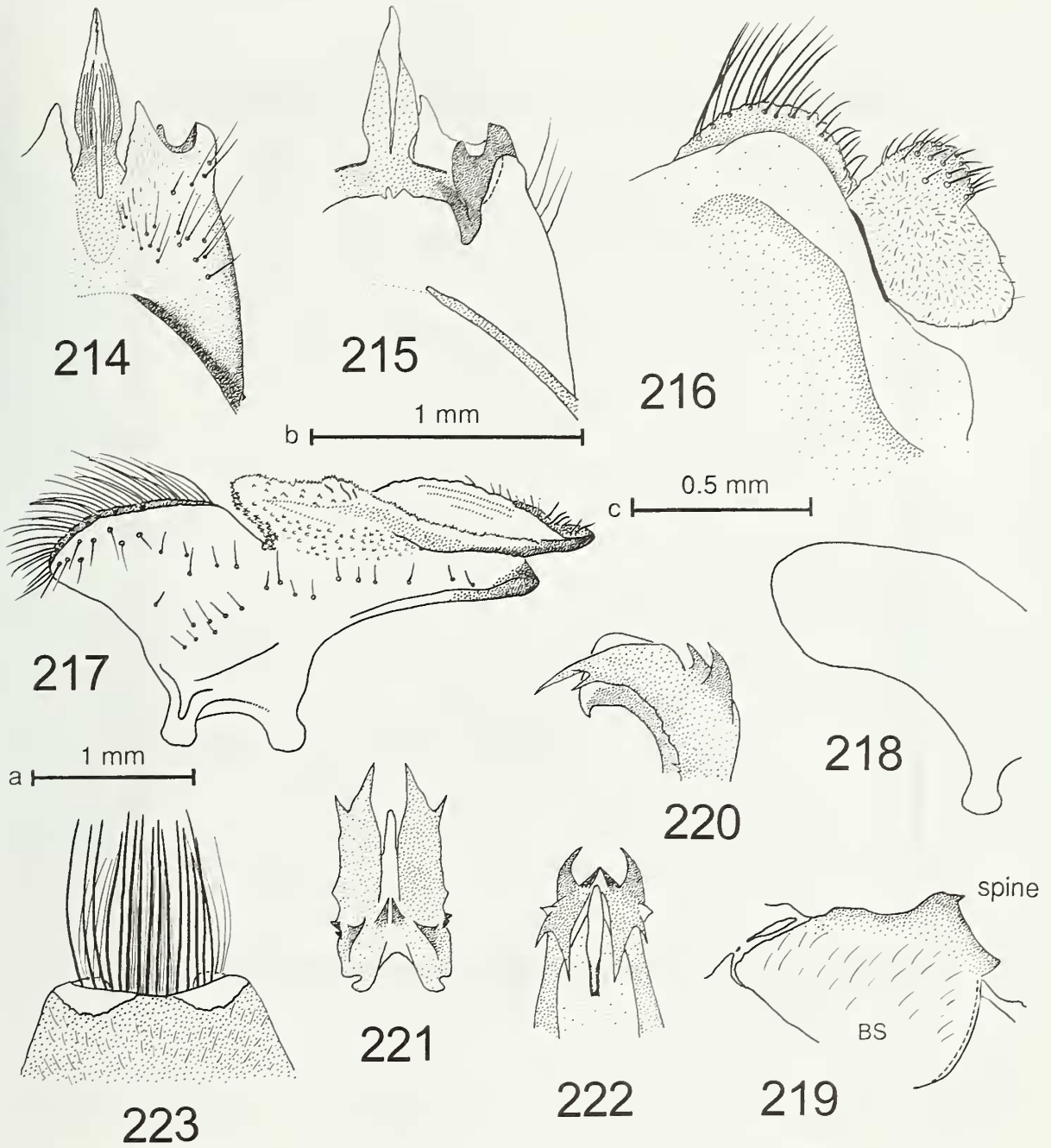
Fig. 204. Distribution of *Tipula (Eremotipula) pellucida* Doane.



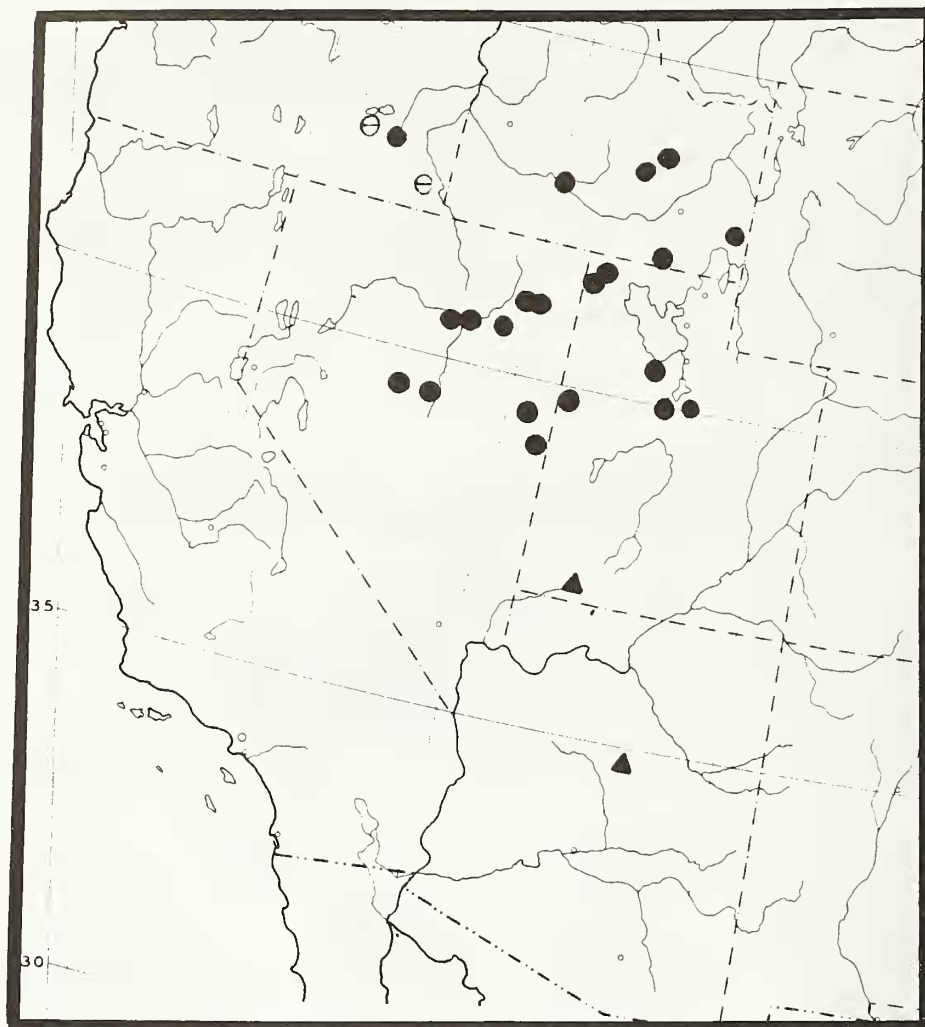
Figs. 205–210. *Tipula (Eremotipula) jicarilla*, n. sp., male. 205, hypopygium, lateral view. 206, 207, ninth tergum, dorsal and ventral views. 208, appendage of ninth sternum and adminiculum, posterior view. 210, inner dististyle, lateral view. 209, adminiculum, dorsal view.



Figs. 211–213. *Tipula* (*Eremotipula*) *jicarilla*, n. sp., female, eighth sternum and hypogynial valves. 211, inner view. 212, dorsolateral view. 213, lateral view.

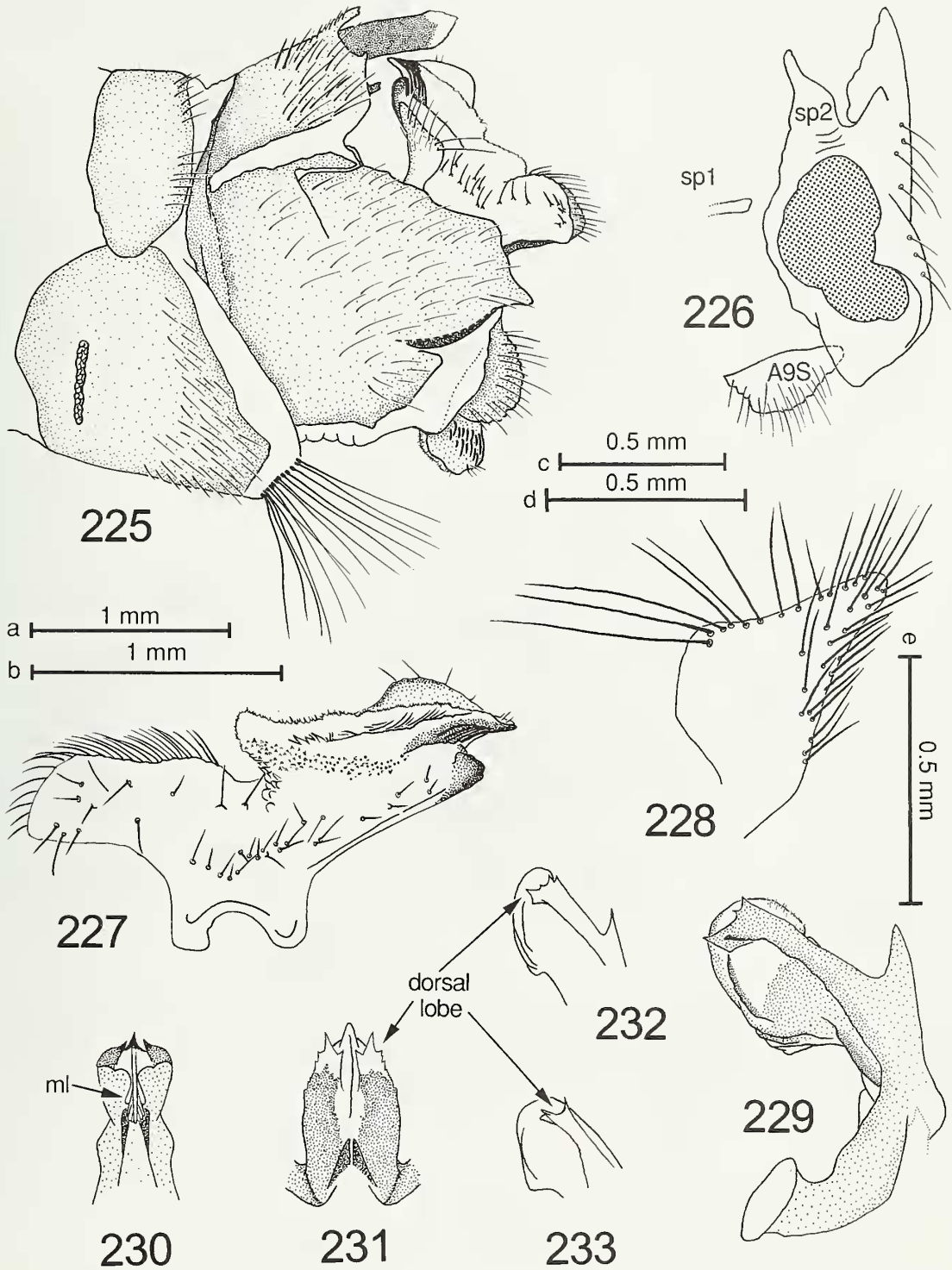


Figs. 214–223. *Tipula* (*Eremotipula*) *byersi*, n. sp., male. 214, 215, ninth tergum, dorsal and ventral views. 216, appendage of ninth sternum, lateral view. 217, inner dististyle, lateral view. 218, outer basal lobe of ID (from paratype slide). 219, spine on basistyle. 220–222, adminiculum, lateral, dorsal and posterior views. 223, apex of eighth sternum. Scale a: 219–223, b: 214–215, 220–222; c: 216–218.

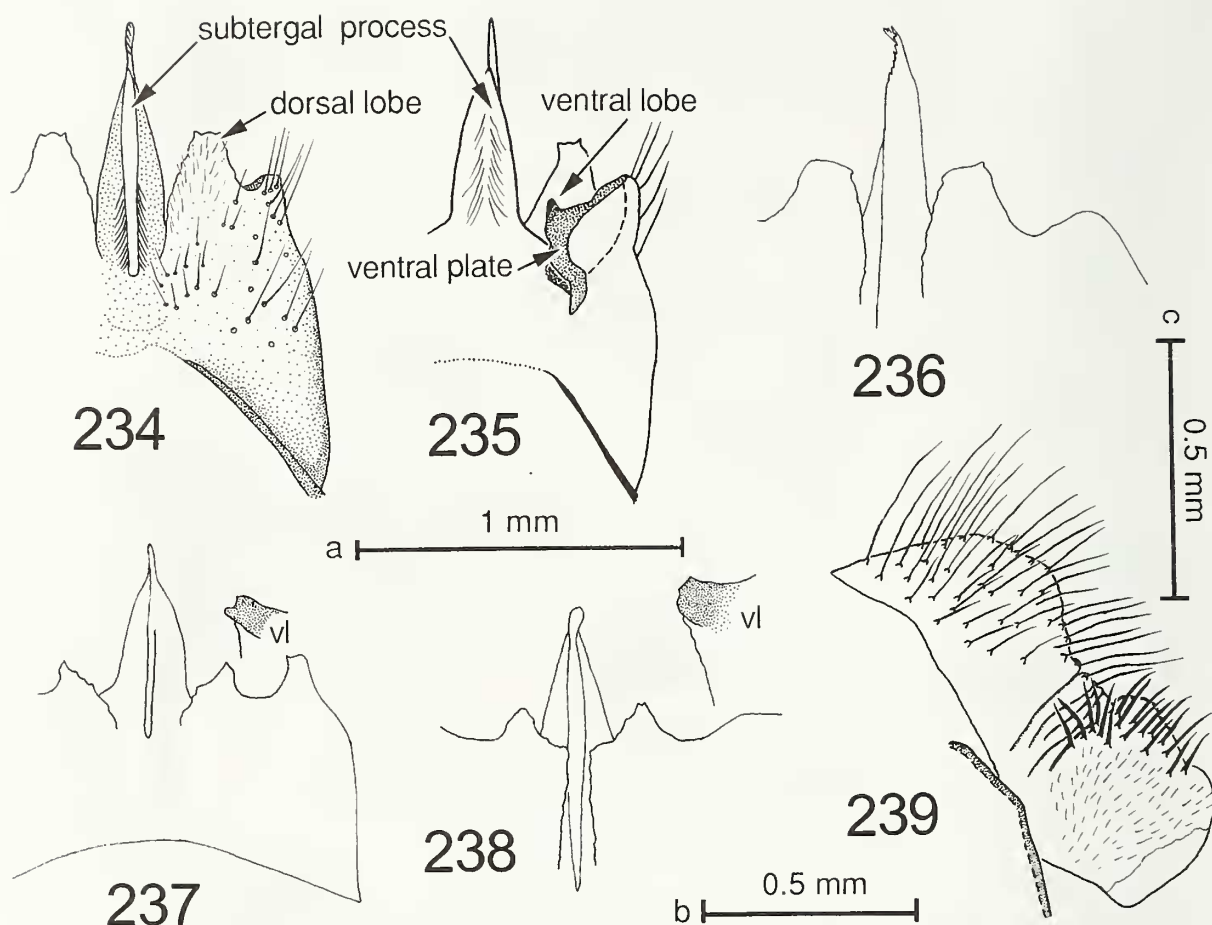


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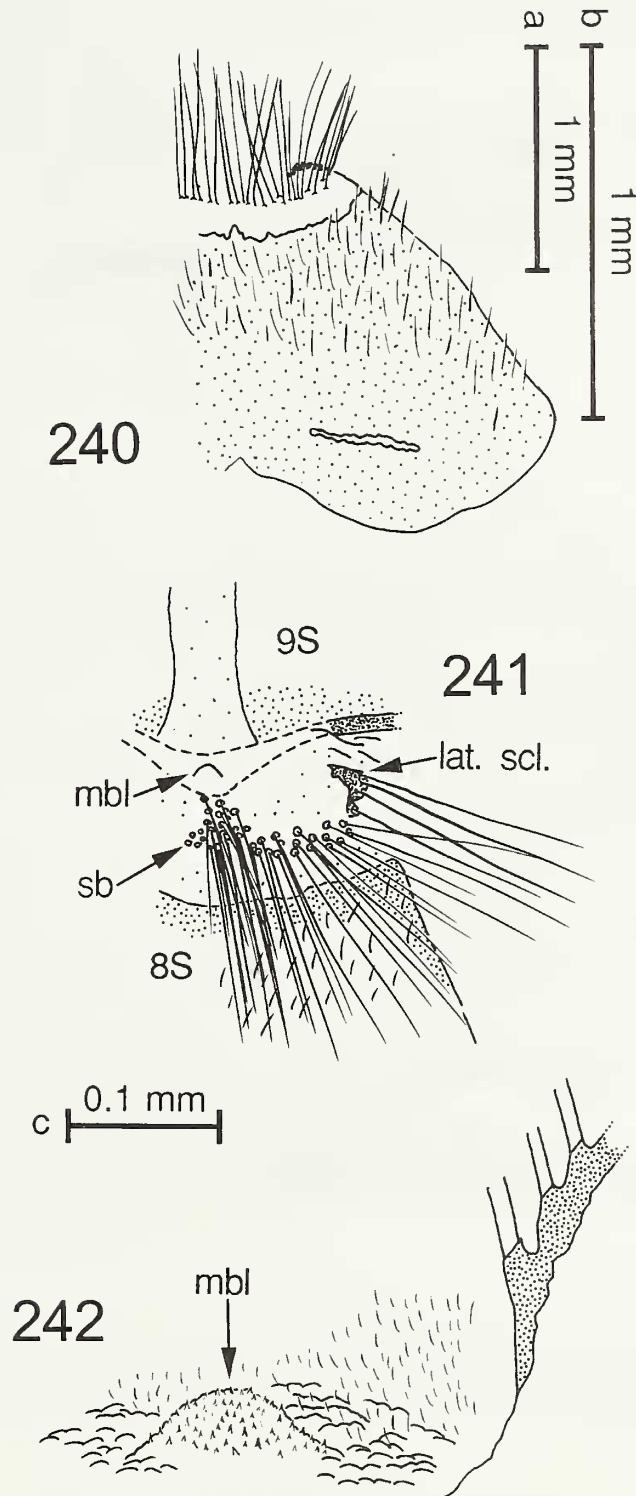
Fig. 224. Distributions of *Tipula* (*Eremotipula*) *byersi*, n. sp. (triangles) and *spaldingi* (circles; divided circle indicates exact locality unknown).



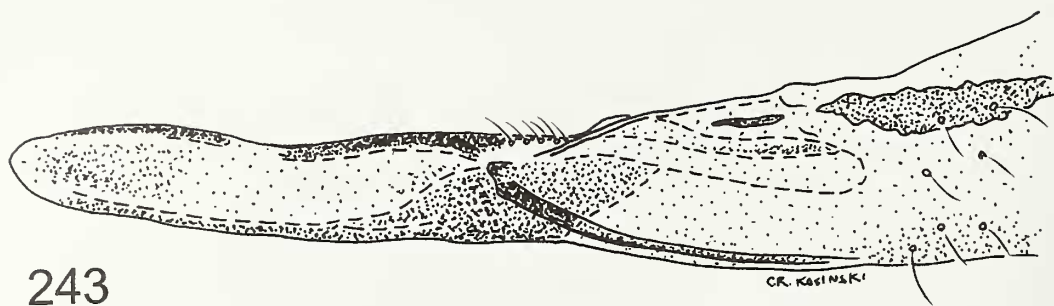
Figs. 225–233. *Tipula (Eremotipula) impudica*, male. 225, hypopygium, lateral view. 226, basistyle, dorsal view (dististyles removed). 227, inner dististyle, lateral view. 228, outer dististyle, lateral view. 229–231, adminiculum, lateral, posterior and dorsal views. *ml* = median lobe. 232, as in Fig. 229, Mancos, Colorado. 233, as in Fig. 229, Kenosha Pass, Colorado. Scale a: 225; b: 226, 230–233; c: 227; d: 229; e: 228.



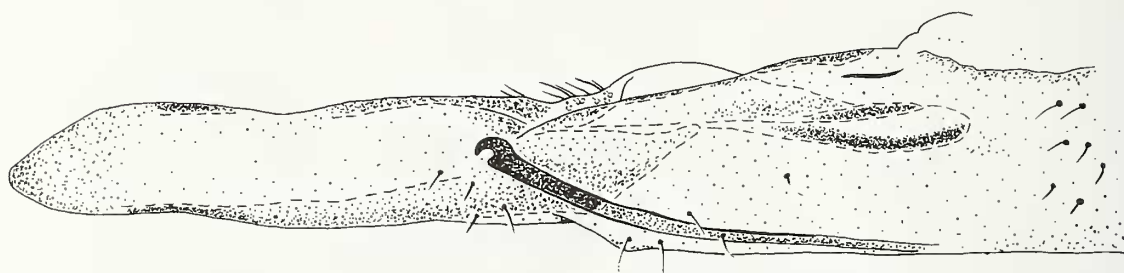
Figs. 234-239. *Tipula (Eremotipula) impudica*, male. 234, 235, ninth tergum, dorsal and ventral views, Snake River, Washington. 236, as in 234, Wawawai, Washington. 237, as in Fig. 234, with inset of ventral lobe, Boulder, Colorado. *vl* = ventral lobe. 238, as in Fig. 237, Colorado (no specific locality). *vl* = ventral lobe. 239, appendage of ninth sternum, lateral view. Scale a: 234-235; b: 236-238; c: 239.



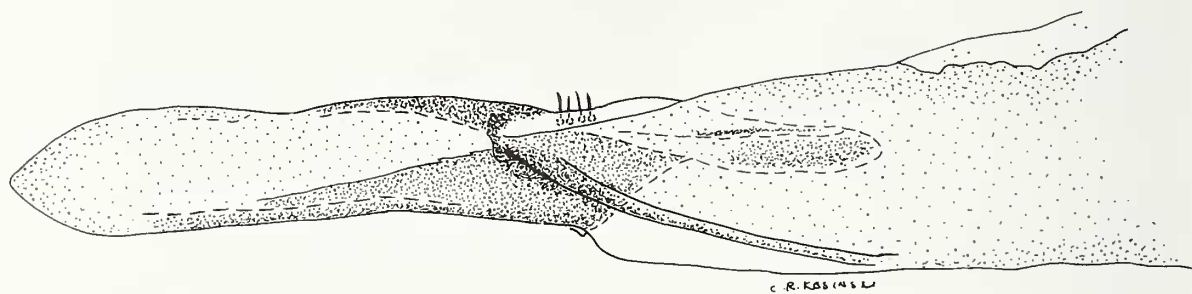
Figs. 240–242. *Tipula (Eremotipula) impudica*, male. 240, eighth sternum (right half shown). 241, intersegmental region between sterna 8 and 9 (right half shown). *lat. scl.* = lateral sclerite; *mbl* = membranous lobe; *sb* = setal band. 242, membranous lobe of eighth sternum. *mbl* = membranous lobe. Scale a: 240; b: 241; c: 242.



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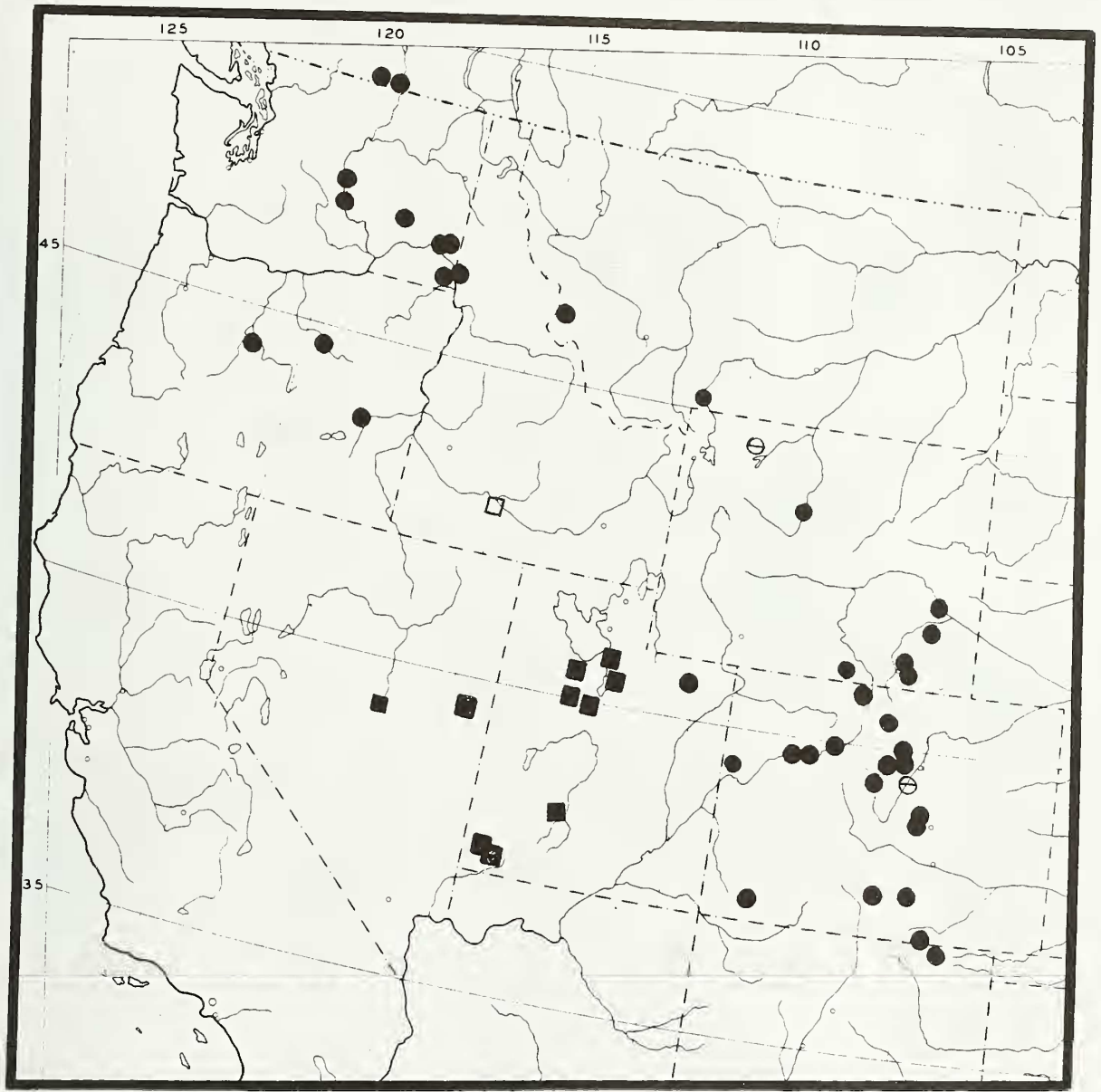


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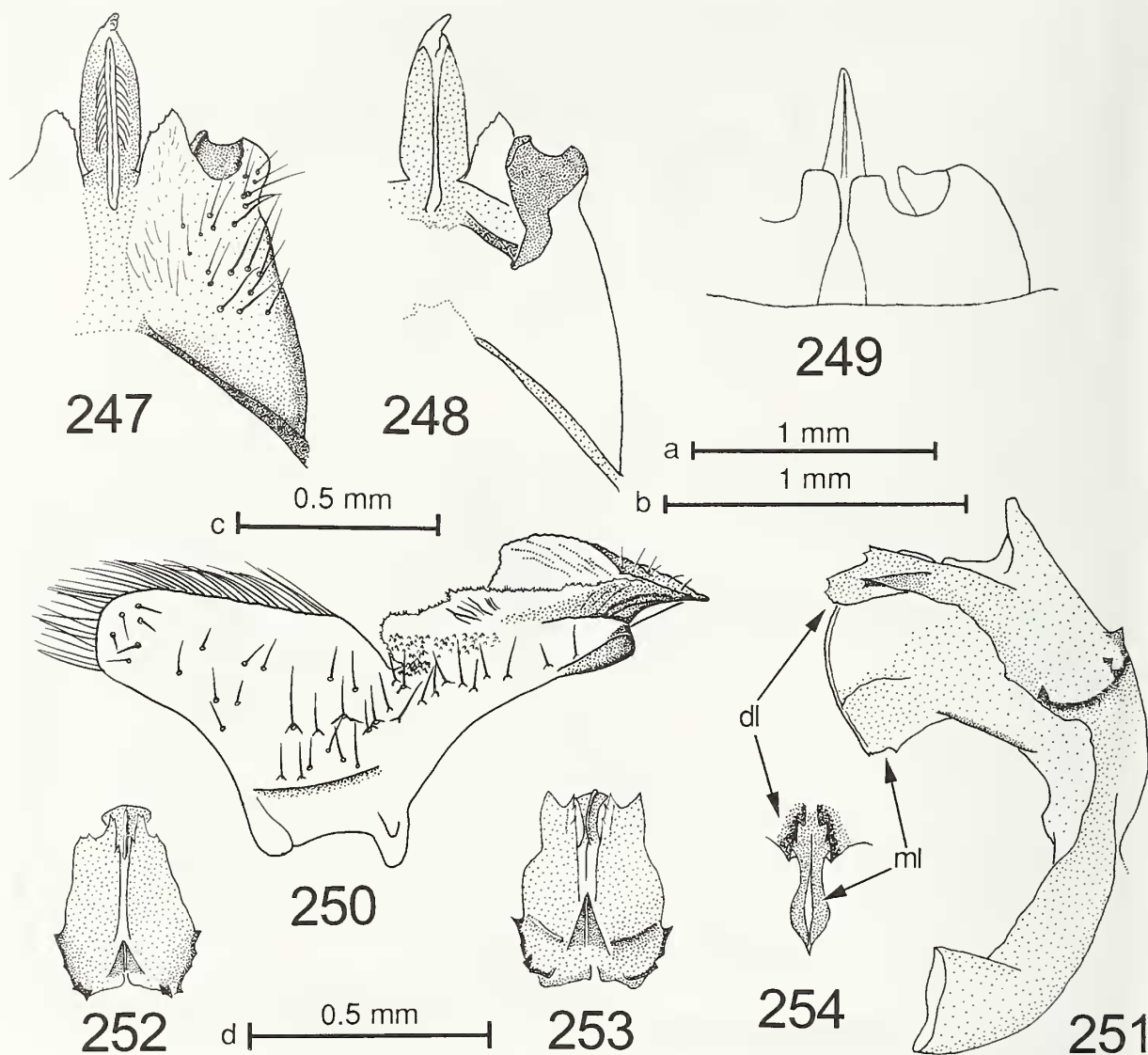
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Figs. 243–245. *Tipula* (*Eremotipula*) *madina* group females, lateral view of eighth sternum and hypogynial valve. 243, *madina*. 244, *spaldingi*. 245, *impudica*.

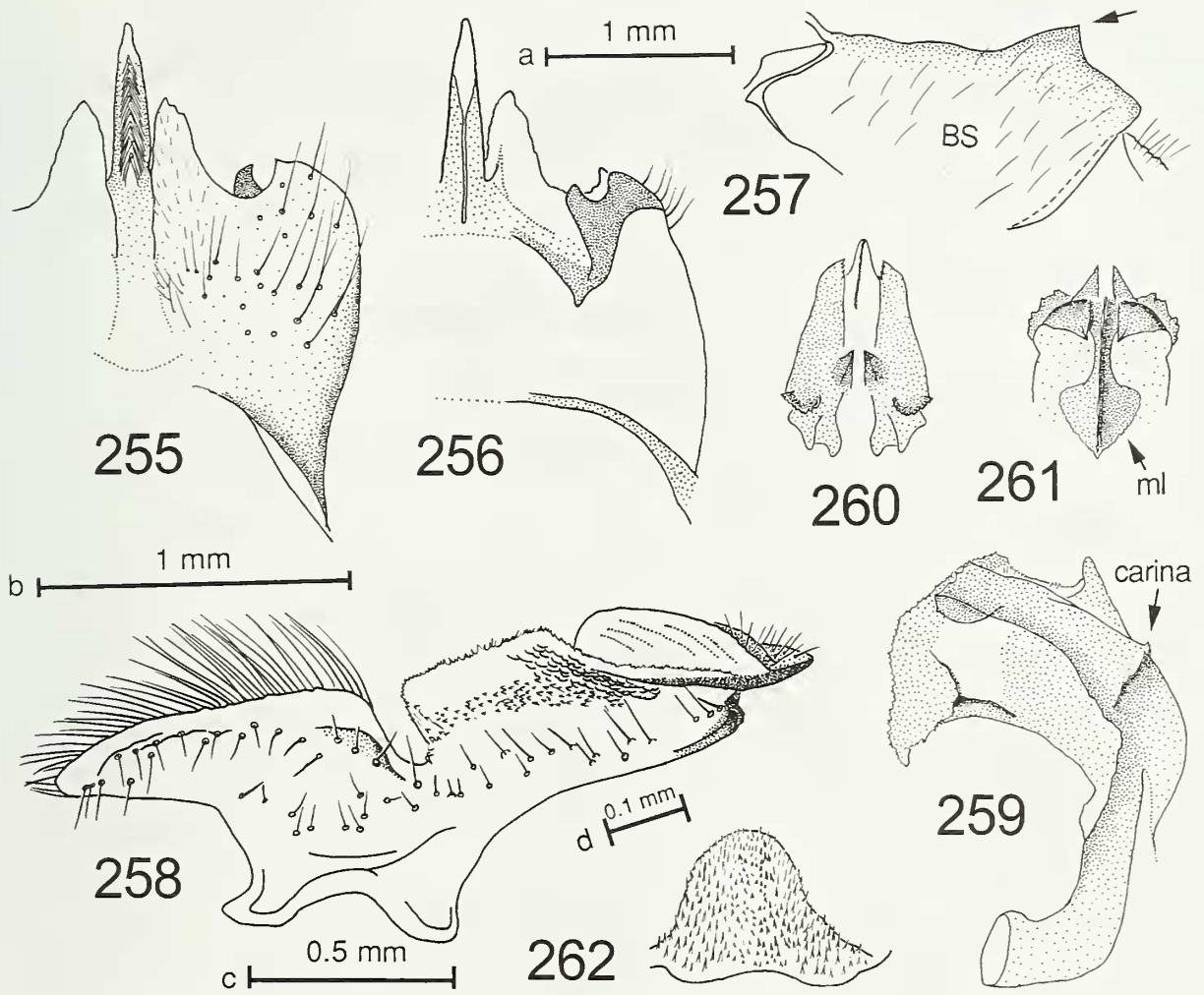


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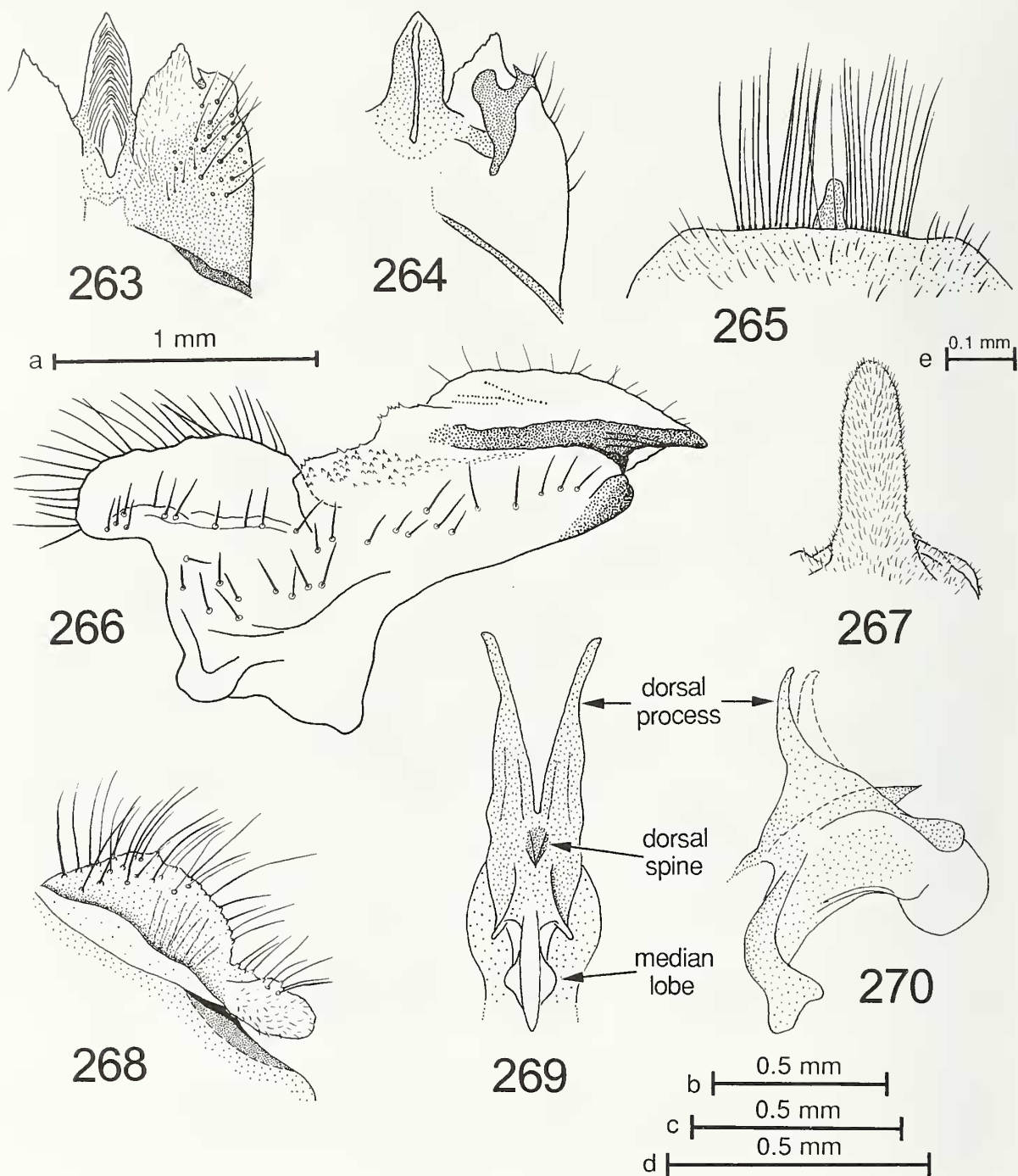
Fig. 246. Distributions of *Tipula (Eremotipula) impudica* Doane (circles, divided circle indicates exact locality unknown) and *madina* Dietz (squares, open square indicates female specimen only).



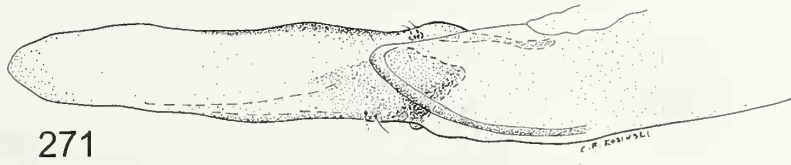
Figs. 247-254. *Tipula (Eremotipula) madina*, male. 247, 248, ninth tergum, dorsal and ventral views. 249, as in Fig. 247, paratype. 250, inner dististyle, lateral view. 251, adminiculum, lateral view, Washington Co., Utah. *dl* = dorsal lobe, *ml* = median lobe. 252, adminiculum, dorsal view, White Pine Co., Nevada. 253, as in Fig. 252, Washington Co., Utah. 254, adminiculum, posterior view. Scale a: 249; b: 247-248, 252-254; c: 250; d: 251.



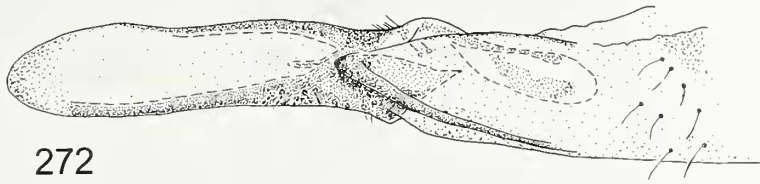
Figs. 255–262. *Tipula (Eremotipula) spaldingi*, male. 255, 256, ninth tergum, dorsal and ventral views. 257, dorsolateral margin of basistyle. 258, inner dististyle, lateral view. 259–261, adminiculum, lateral, dorsal and posterior views. *ml* = median lobe. 262, membranous lobe of eighth sternum. Scale a: 257; b: 255–256, 260–261; c: 258–259; d: 262.



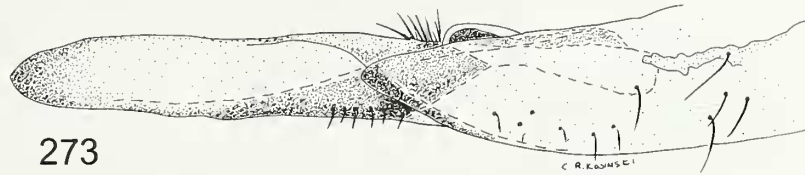
Figs. 263–270. *Tipula (Eremotipula) anasazi*, male. 263, 264, ninth tergum, dorsal and ventral views. 265, appendage of ninth sternum, lateral view. 266, inner dististyle, lateral view. 267, membranous lobe of eighth sternum. 268, apex of eighth sternum. 269, 270, adminiculum, dorsal and lateral views. Scale a: 263–264, 268; b: 270; c: 265; d: 266, 269; e: 267.



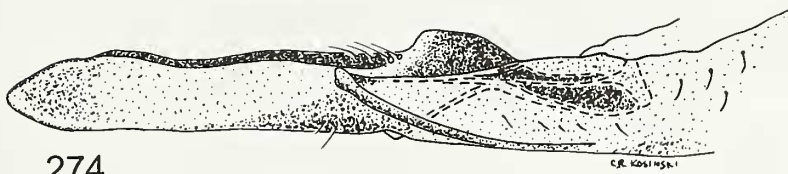
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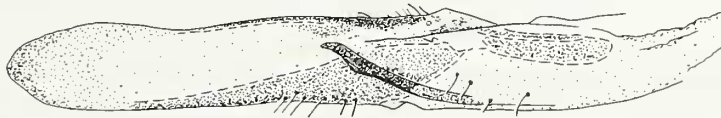
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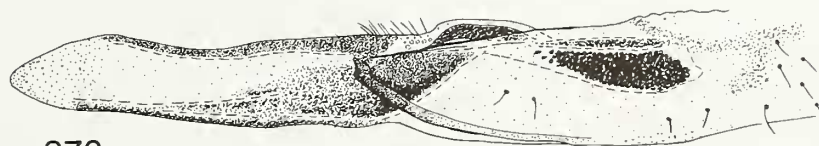
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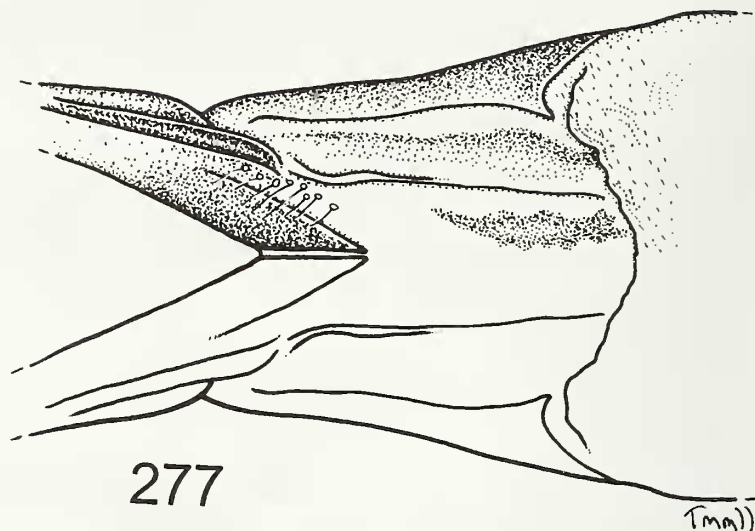


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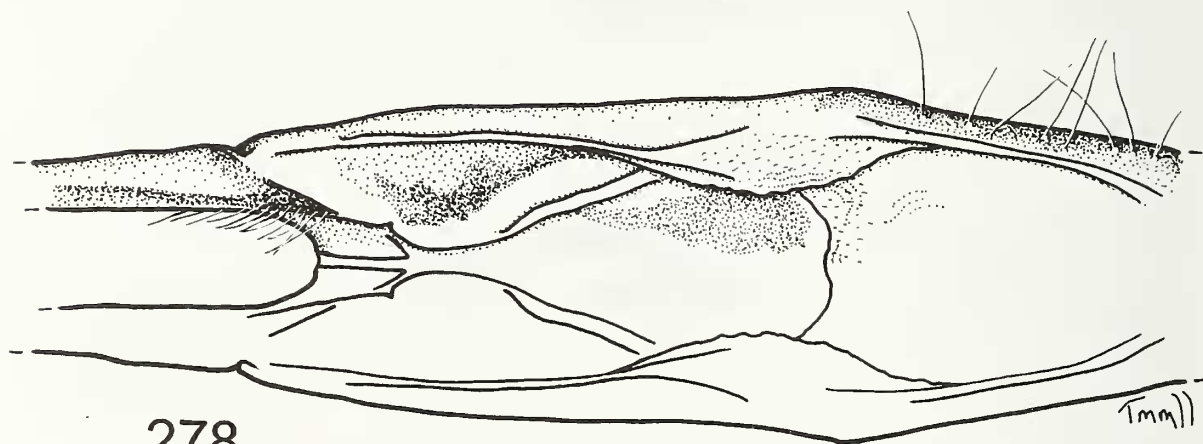
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Figs. 271–276. *Tipula* (*Eremotipula*) *kaibabensis* group and *artemisiae* females, lateral view of eighth sternum and hypogynial valve. 271, *artemisiae*. 272, *dimidiata*. 273, *anasazi*. 274, *kaibabensis*. 275, *mitrata*, Arizona: Grand Canyon. 276, *mitrata*, Arizona: Gila Co.



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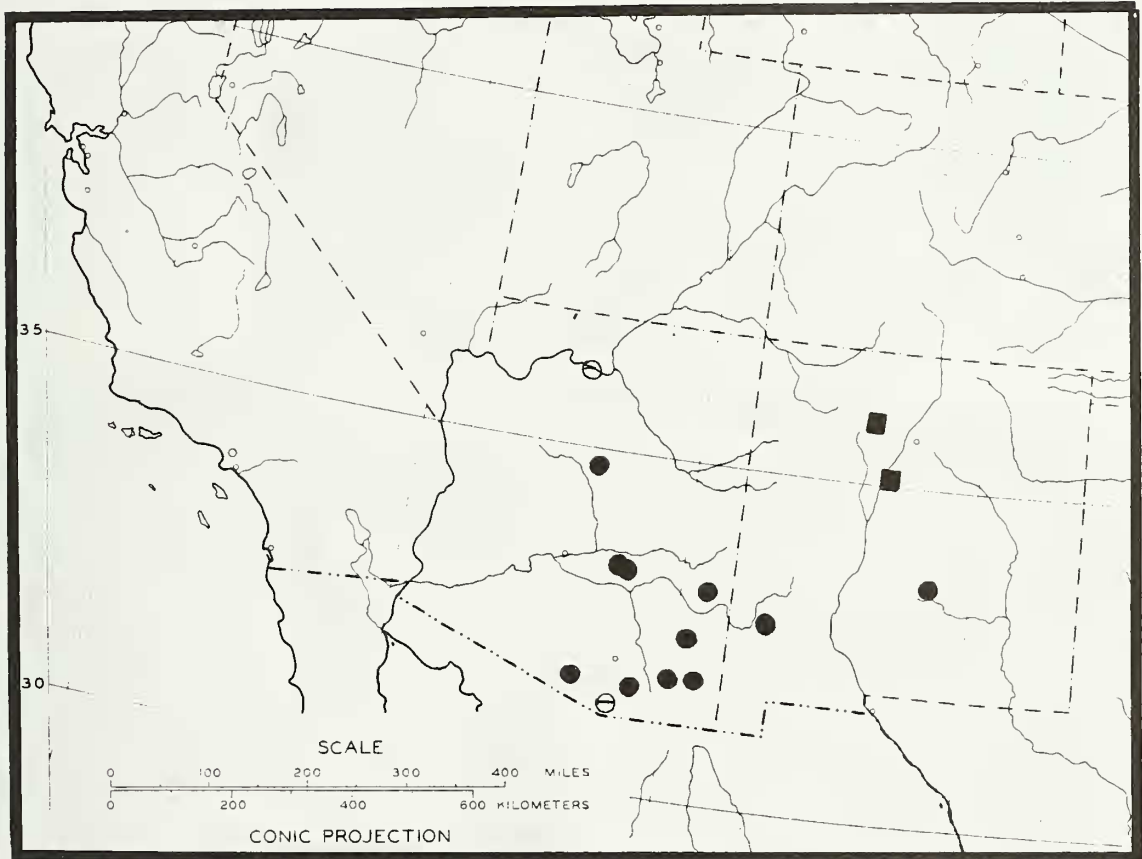
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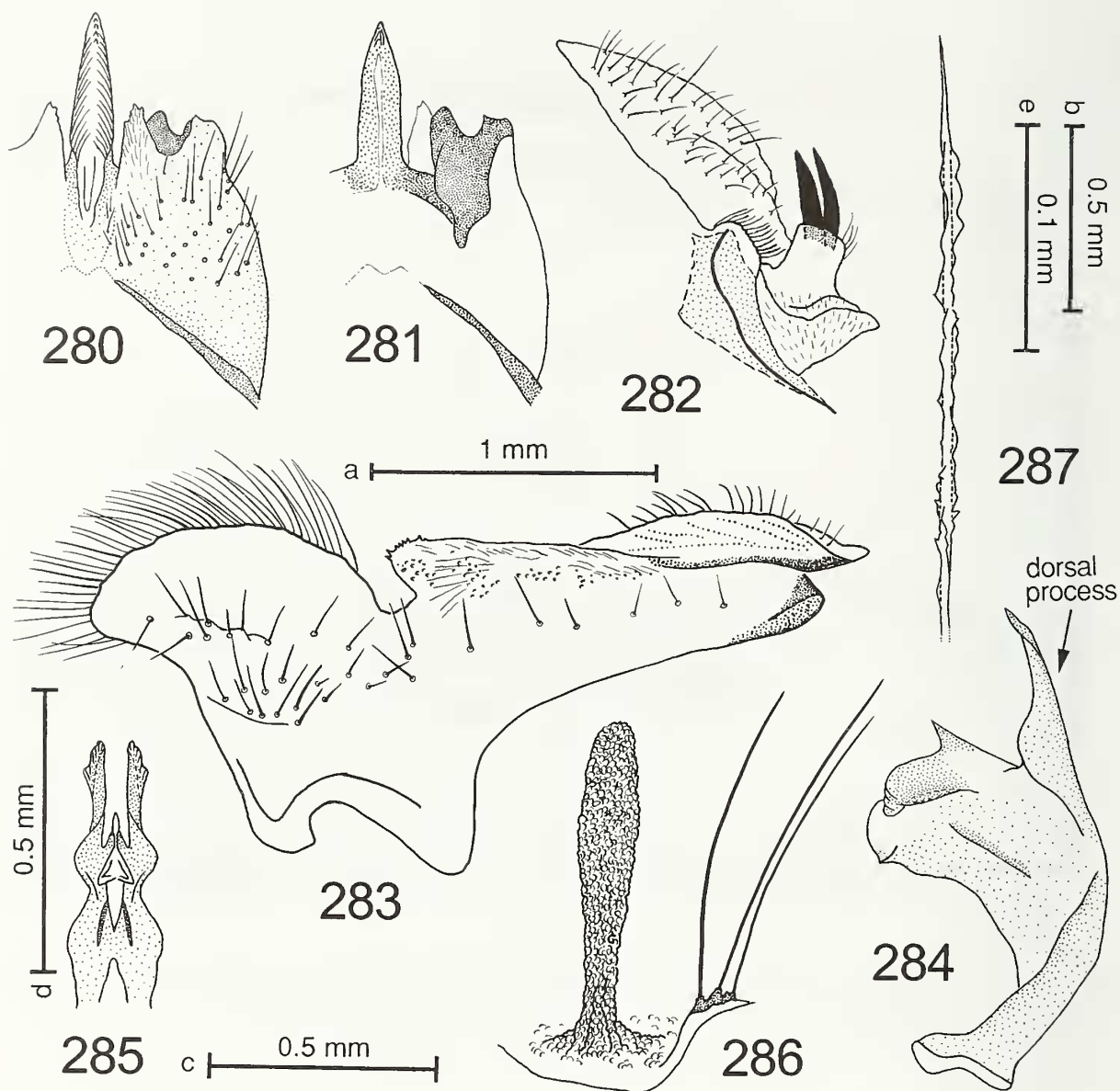
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Figs. 277–278. *Tipula* (*Eremotipula*) *kaibabensis* group females, dorsal (inner) view of eighth sternum and hypogynial valve. 277, *dimidiata*. 278, *anasazi*.

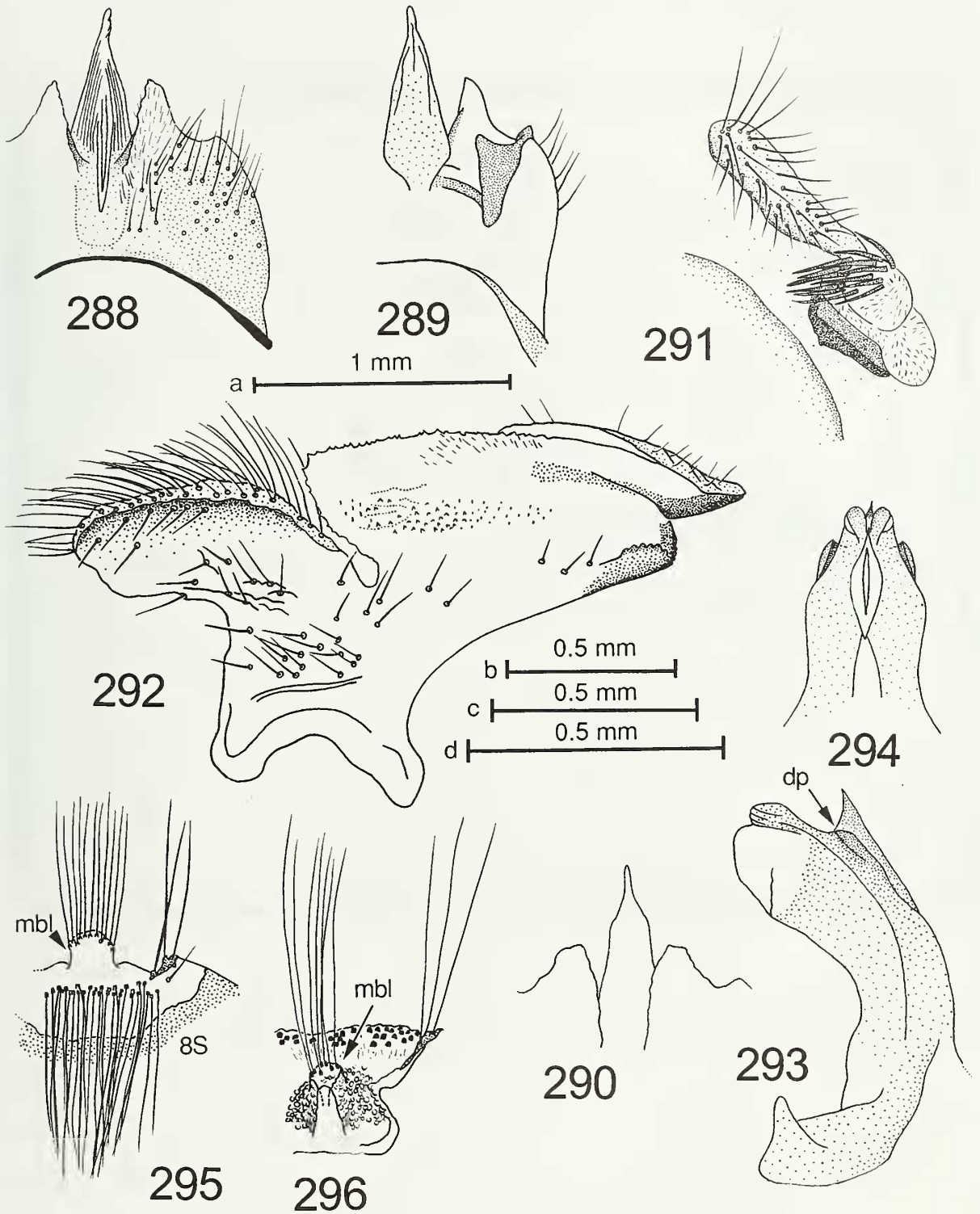


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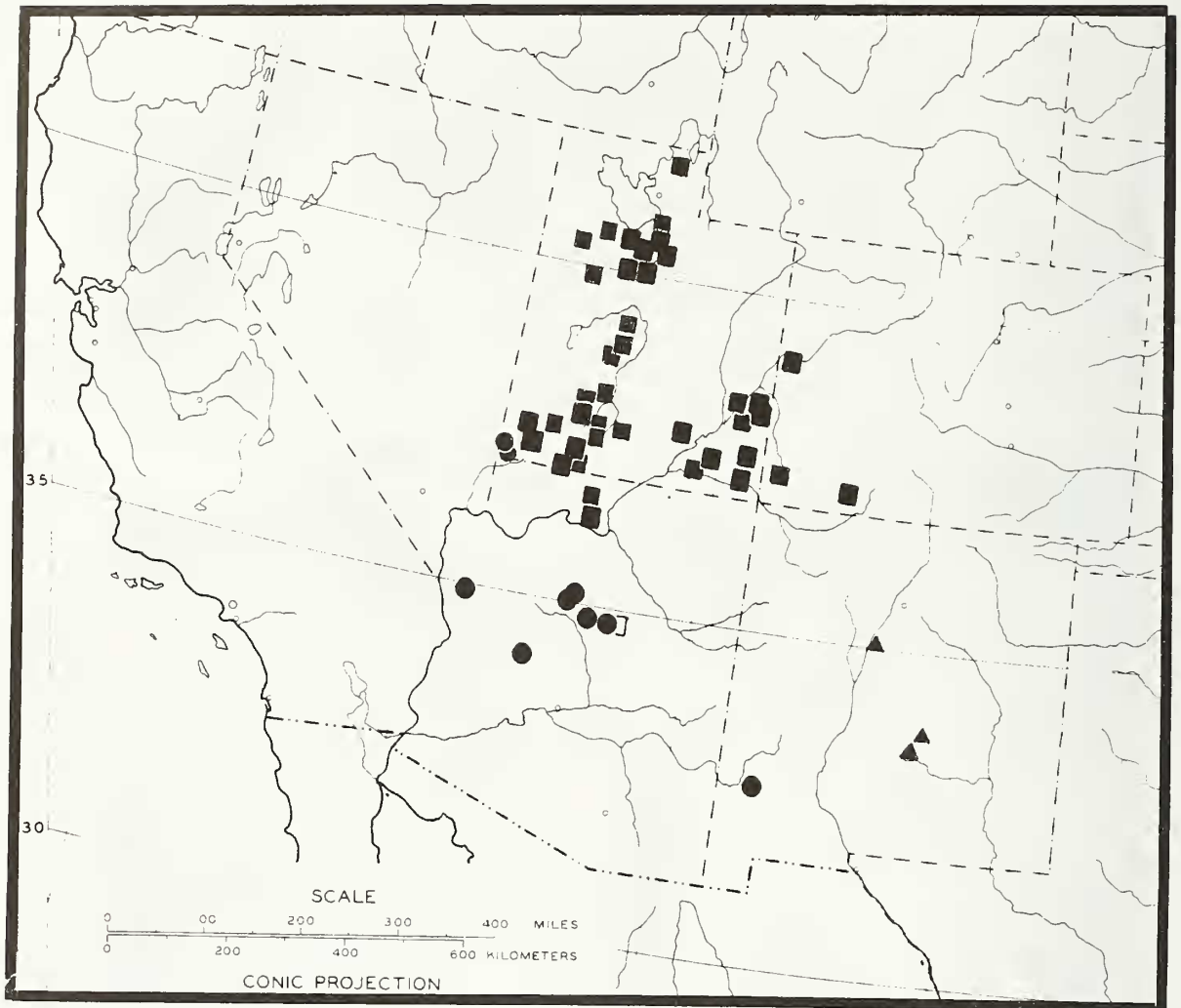
Fig. 279. Distributions of *Tipula (Eremotipula) anasazi*, n. sp. (squares) and *mitrata* Dietz (circles, divided circle indicates exact locality unknown).



Figs. 280–287. *Tipula (Eremotipula) nitrata*, male. 280, 281, ninth tergum, dorsal and ventral views. 282, appendage of ninth sternum, lateral view. 283, inner dististyle, lateral view. 284, 285, adminiculum, lateral and posterior views. 286, membranous lobe of eighth sternum, inner view. 287, seta from eighth sternum band. Scale a: 280–281, 285; b: 284, 286; c: 282; d: 283; e: 287.

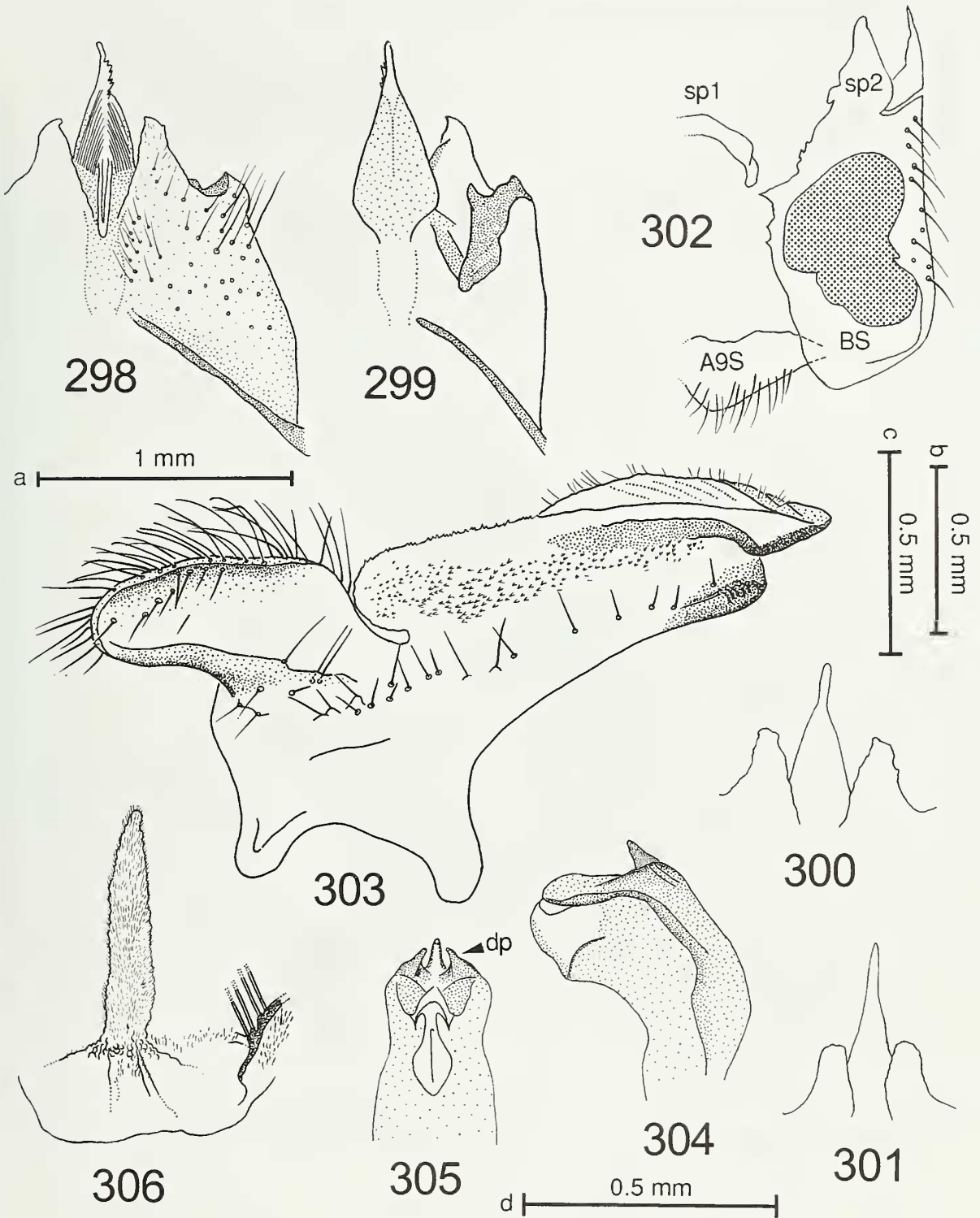


Figs. 288–296. *Tipula (Eremotipula) dimidiata*, male. 288, 289, ninth tergum, dorsal and ventral views. 290, as in 288, Double Springs Camp, Arizona. 291, appendage of ninth sternum, dorsolateral view. 292, inner dististyle, lateral view. 293, 294, adminiculum, lateral and posterior views. 295, 296, eighth sternum and membranous lobe, outer and inner views. *mbl* = membranous lobe. Scale a: 288–290, 295; b: 296; c: 291; d: 292, 294.

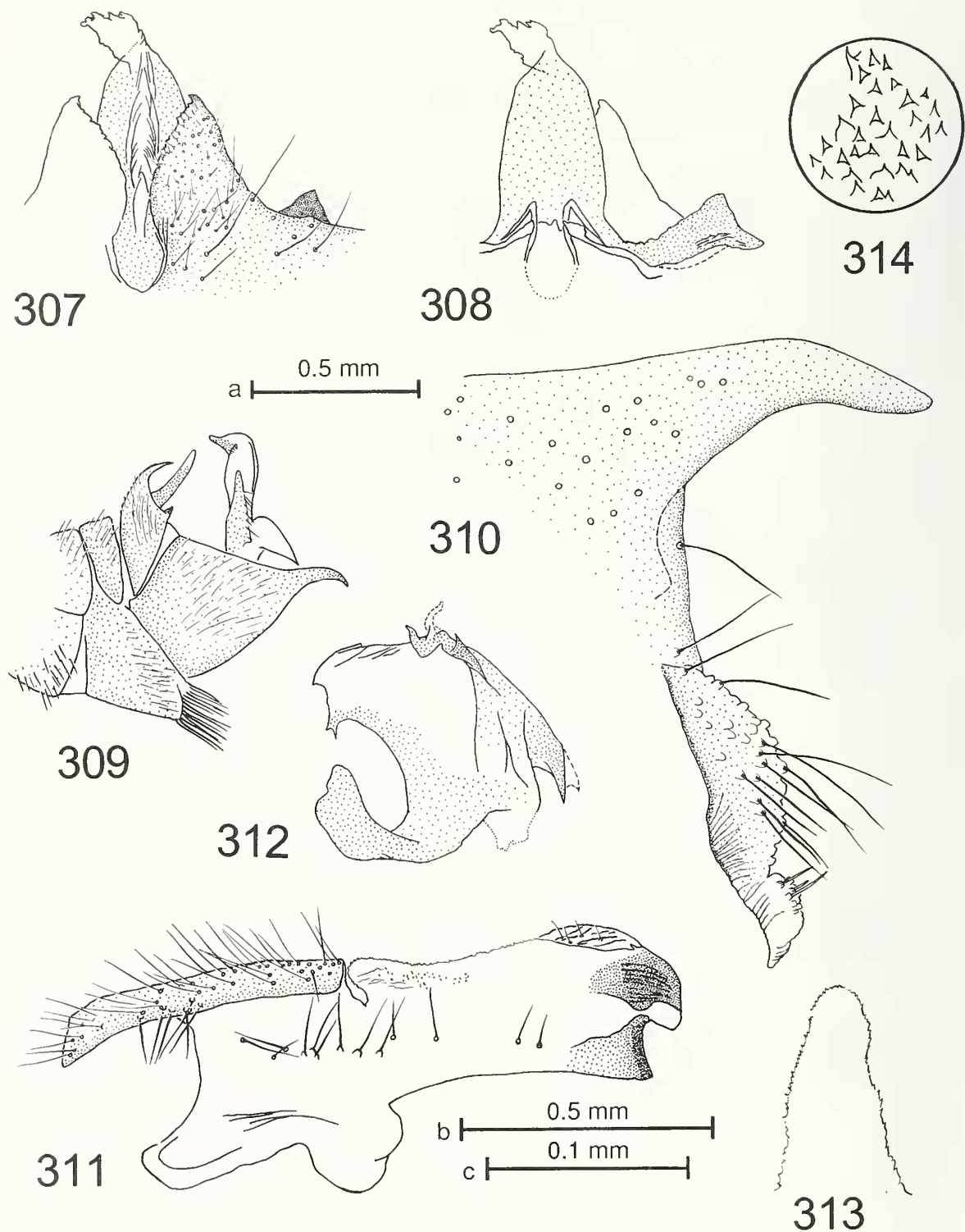


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Fig. 297. Distributions of *Tipula* (*Eremotipula*) *dimidiata* Dietz (circles), *kaibabensis* Alexander (squares; open square indicates record based on female specimen only) and *jicarilla*, n. sp. (triangles).



Figs. 298–306. *Tipula (Eremotipula) kaibabensis*, male. 298, 299, ninth tergum, dorsal and ventral views. 300, 301, outline of ninth tergum, dorsal view. 302, basistyle, dorsal view (dististyles removed). 303, inner dististyle, lateral view. 304, 305, adminiculum, lateral and posterior views. *dp* = dorsal process. 306, membranous lobe of eighth sternum, inner view. Scale a: 298–302; b: 305–306; c: 304; d: 303.



Figs. 307–314. *Tipula (Eremotipula) biproducta*, male. 307, 308, ninth tergum, dorsal and ventral views. 309, hypopygium, lateral view. 310, basistylar horn and the appendage of the ninth sternum, lateral view. 311, inner dististyle, lateral view. 312, adminiculum, lateral view. 313, membranous lobe of eighth sternum, outline. 314, detail of surface of membranous lobe. Scale a: 311–312; b: 307–308, 310, 313; c: 314.

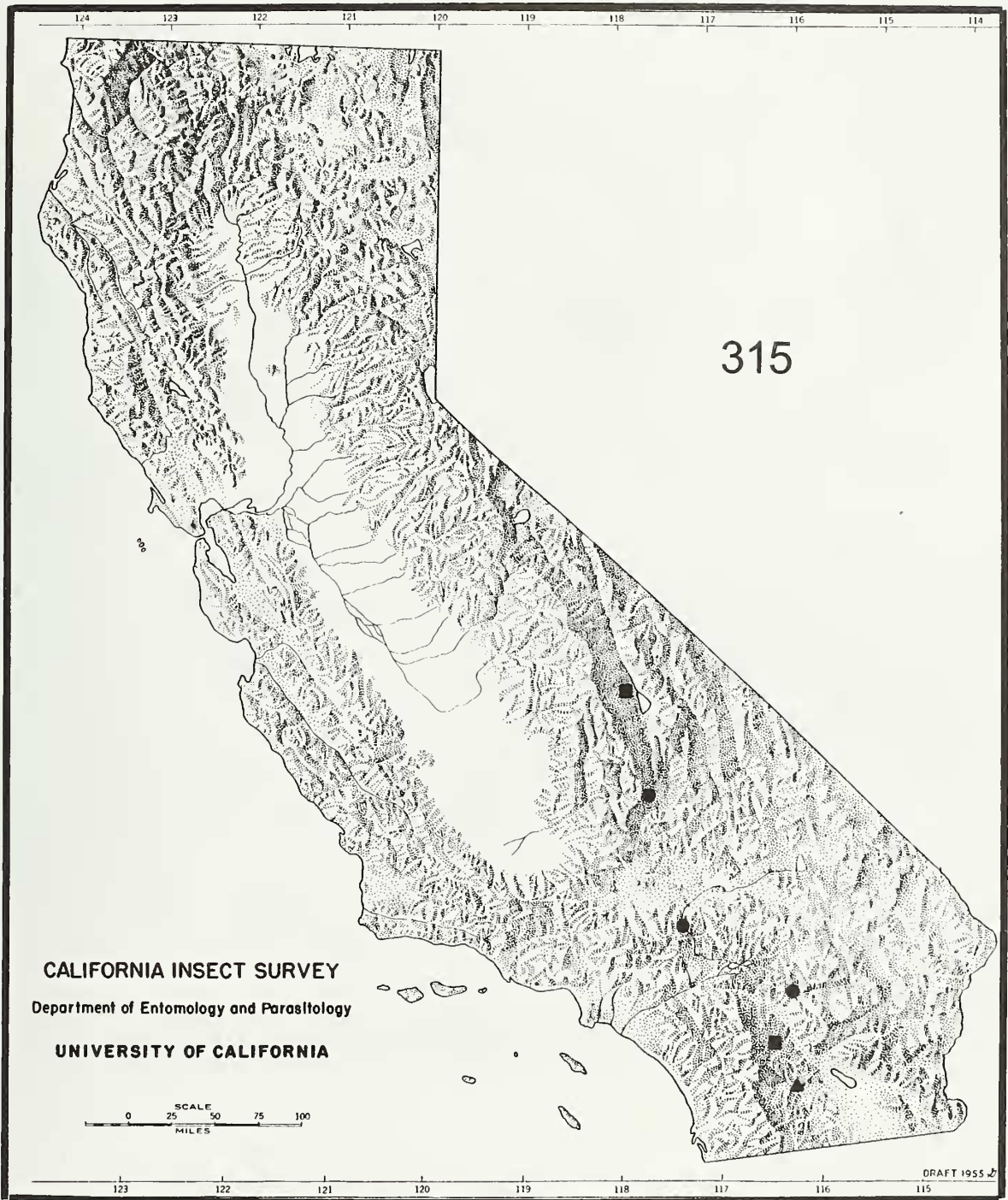
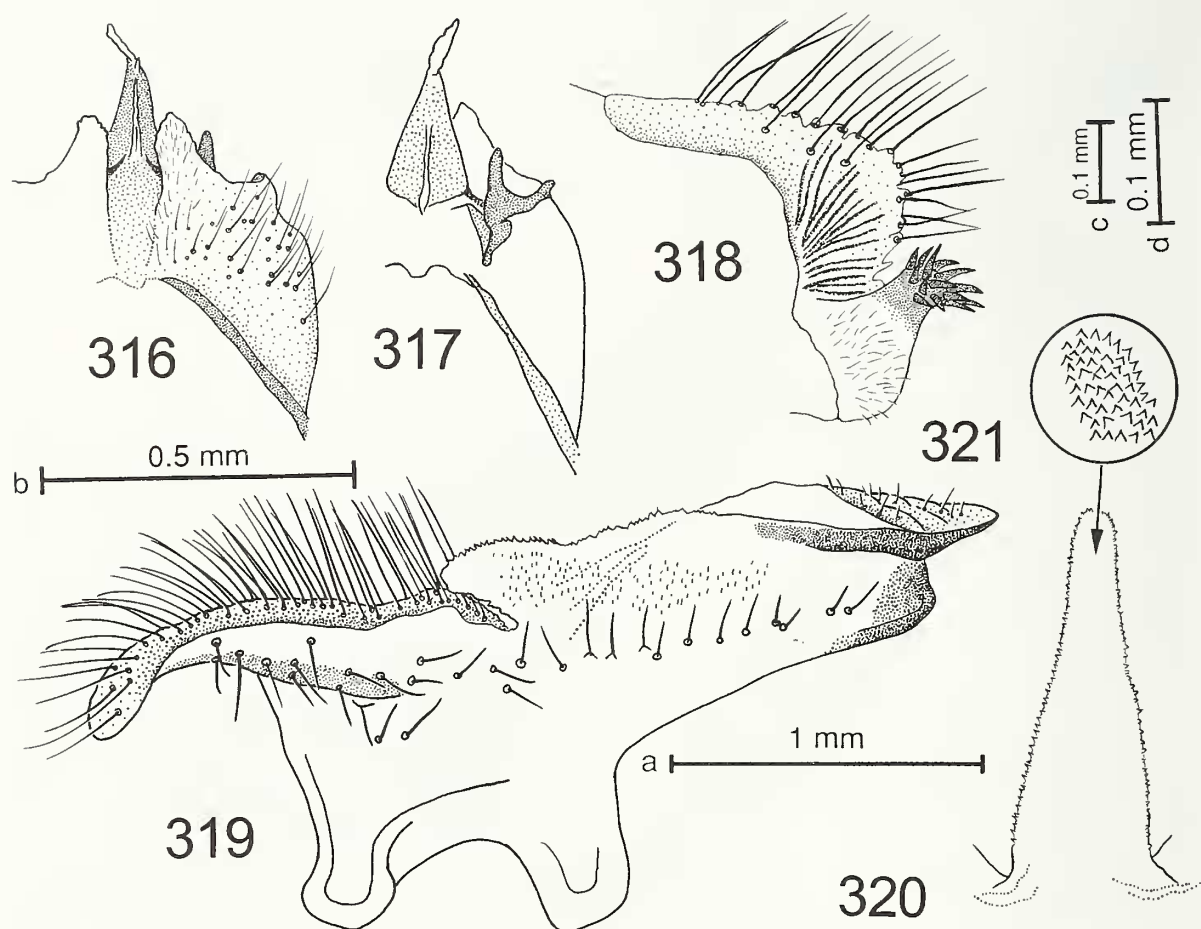
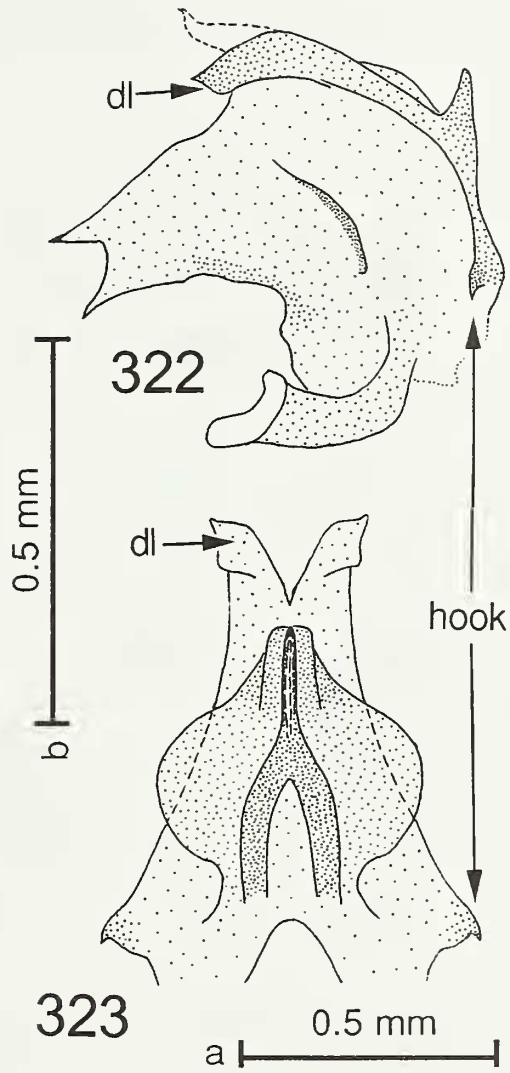


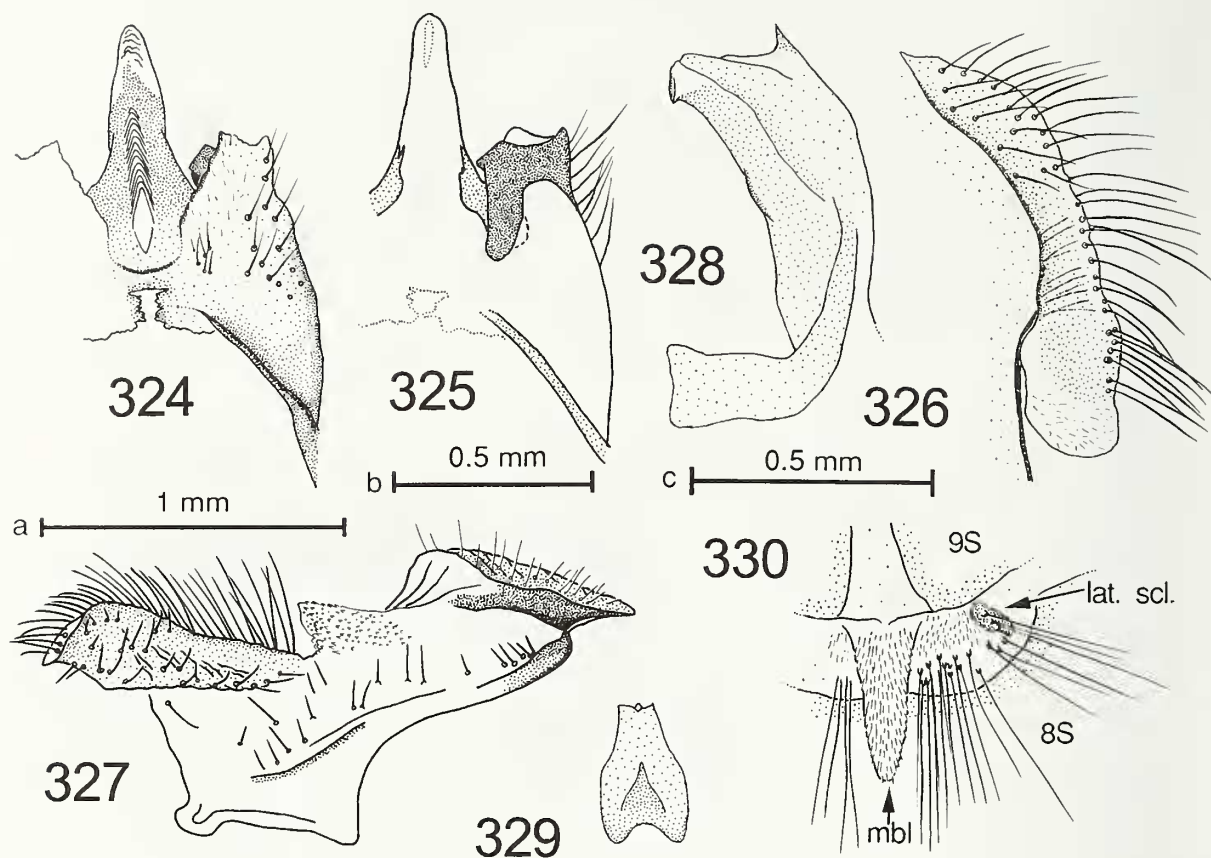
Fig. 315. Distributions of *Tipula* (*Eremotipula*) *biproducta* Alexander (triangle), *schusteri* Alexander (circles) and *spinosa*, n. sp. (squares).



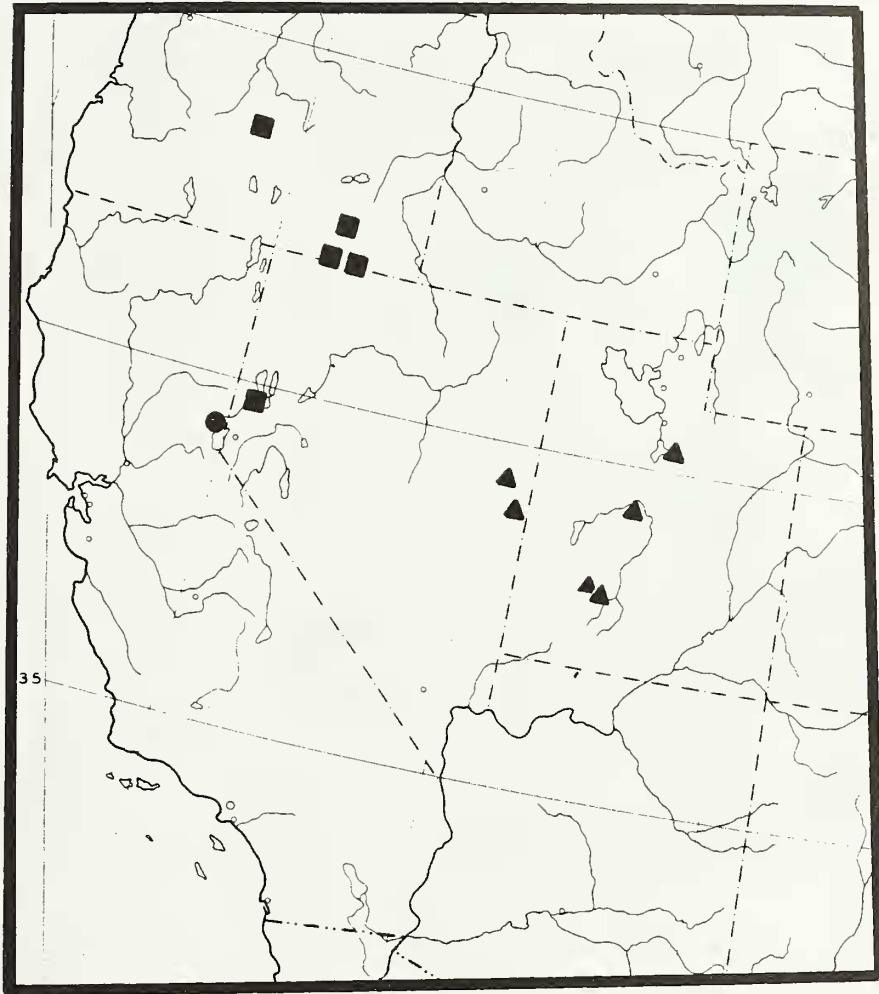
Figs. 316–321. *Tipula (Eremotipula) spinosa*, male. 316, 317, ninth tergum, dorsal and ventral views. 318, appendage of ninth sternum, lateral view. 319, inner dististyle, lateral view. 320, membranous lobe of eighth sternum, outline. 321, detail of surface of the membranous lobe. Scale a: 316–317; b: 318–319; c: 320; d: 321.



Figs. 322–323. *Tipula (Eremotipula) spinosa*, male adminiculum, lateral and posterior views. *dl* = dorsal lobe. Scale a: 322; b: 323.

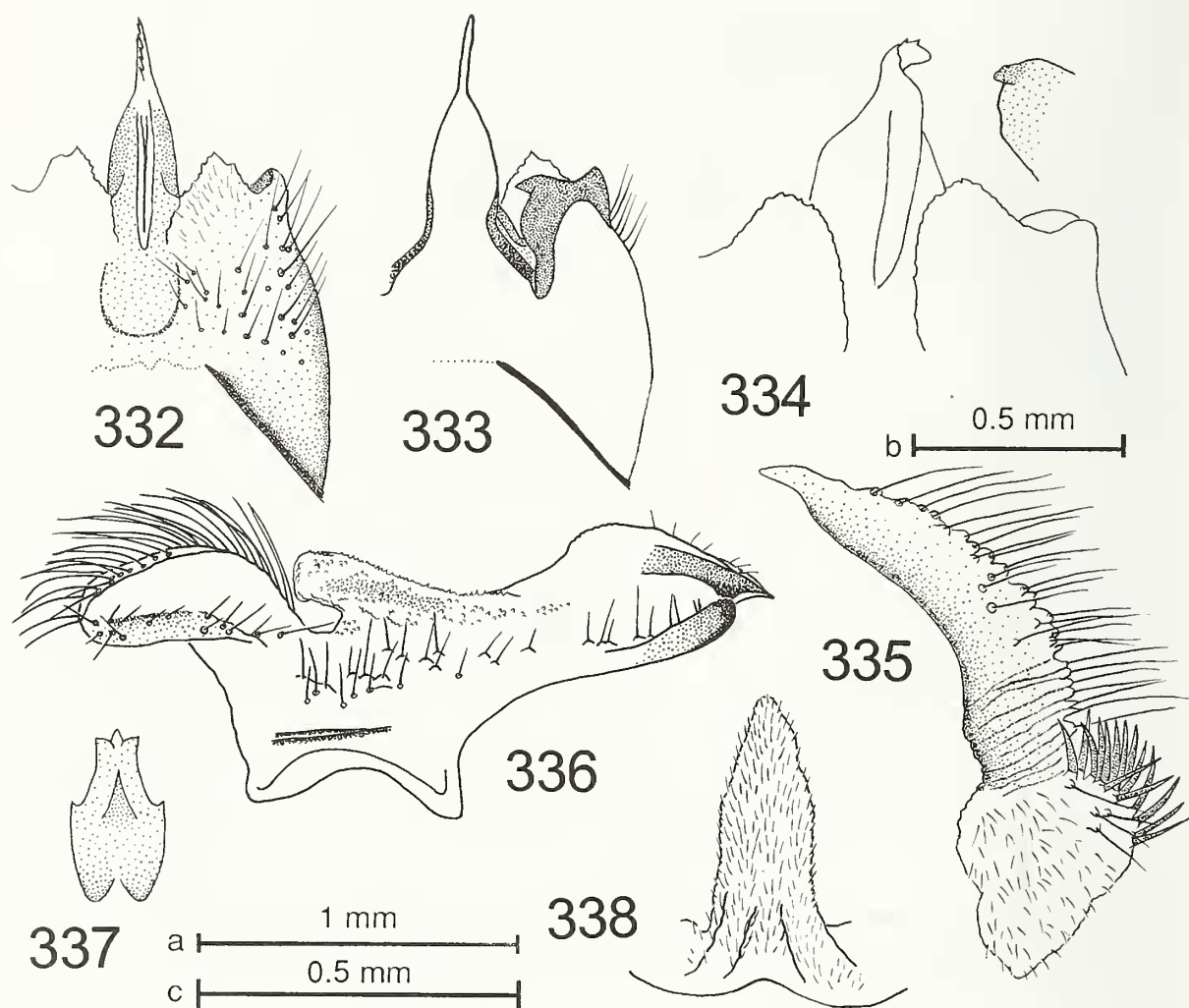


Figs. 324–330. *Tipula (Eremotipula) woodi*, male. 324, 325, ninth tergum, dorsal and ventral views. 326, appendage of ninth sternum, lateral view. 327, inner dististyle, lateral view. 328, 329, adminiculum, lateral and dorsal views. 330, intersegmental region between eighth and ninth sterna, with membranous lobe. *lat.scl.* = lateral sclerite, *mbl* = membranous lobe. Scale a: 324–325, 209–210; b: 327–328; c: 326.

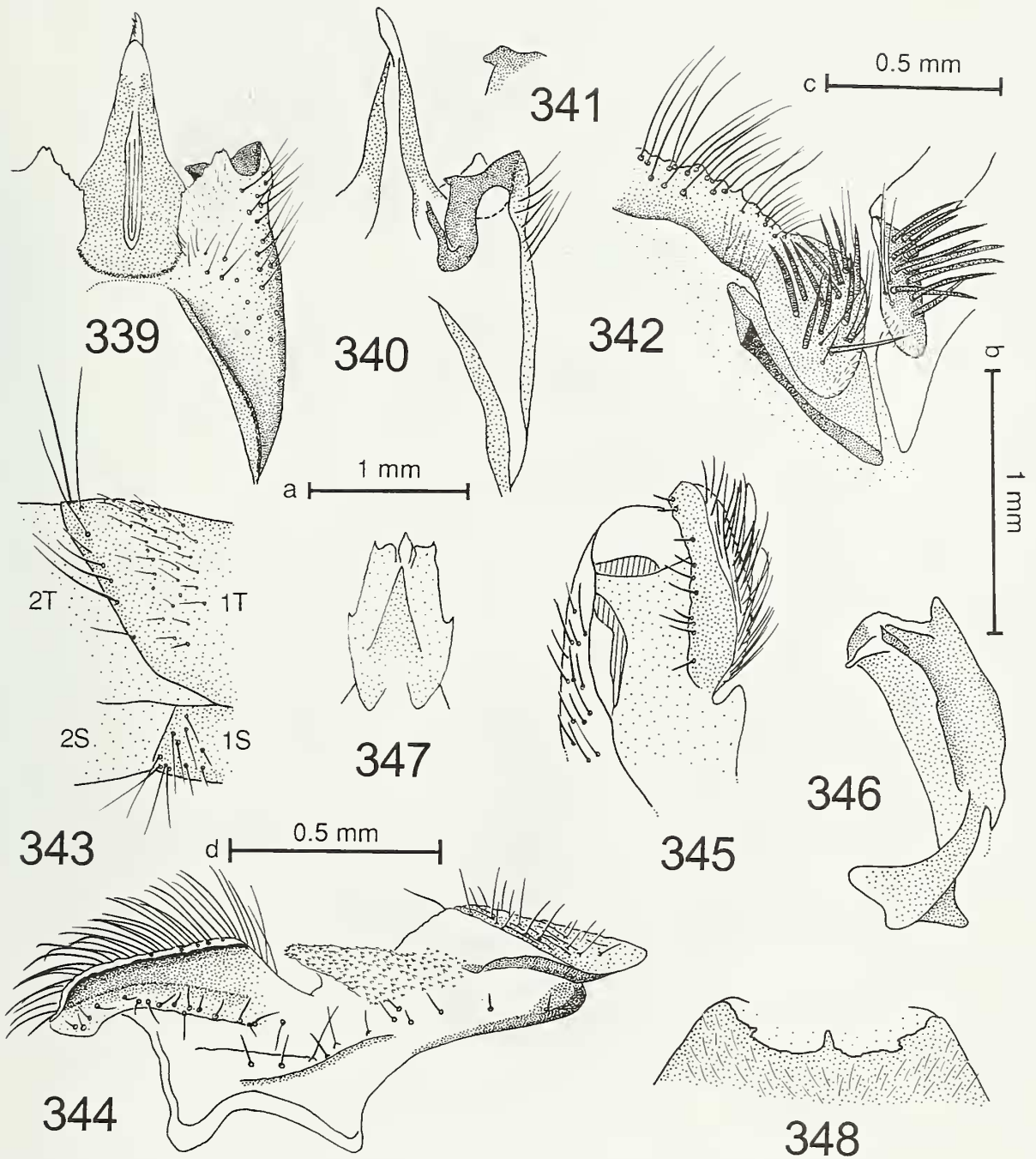


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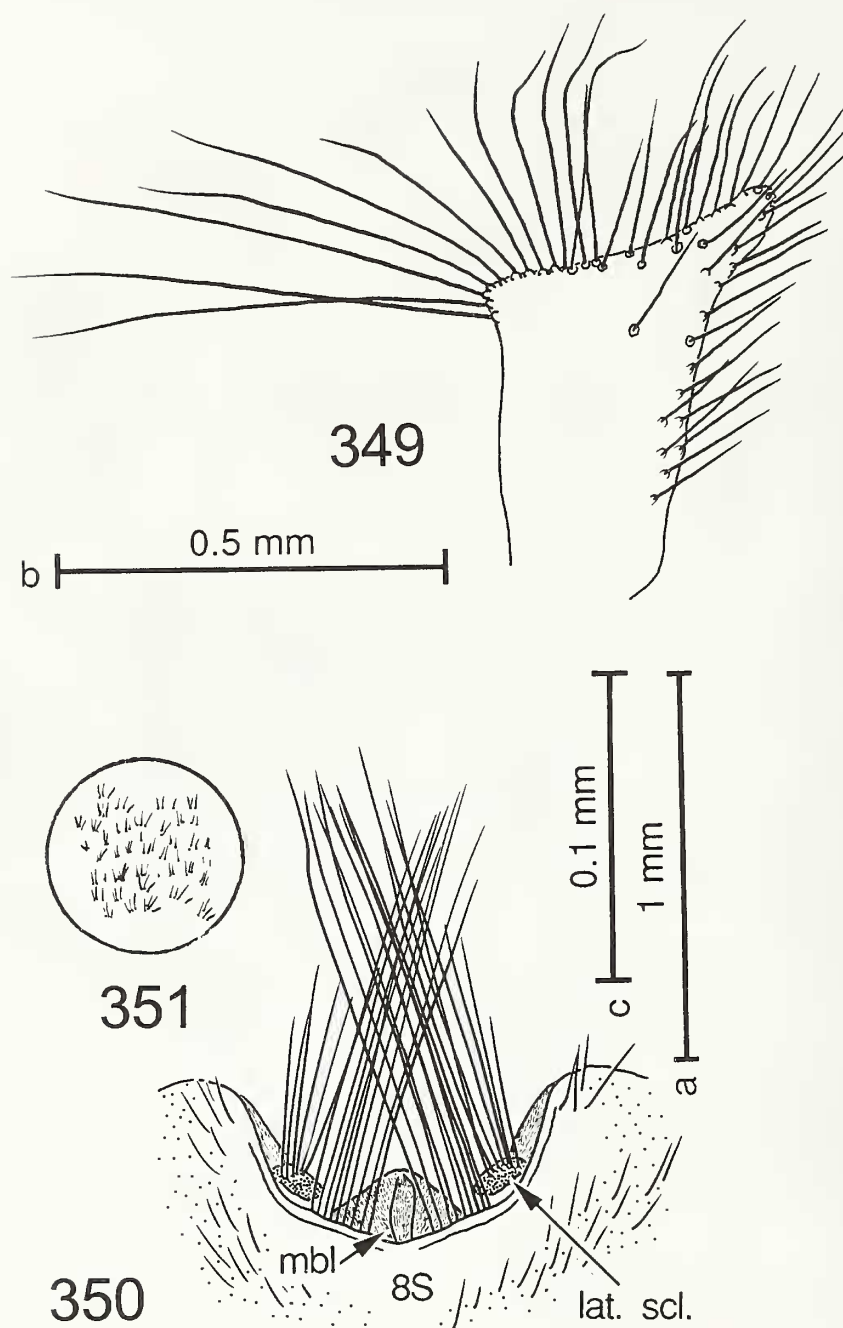
Fig. 331. Distributions of *Tipula (Eremotipula) artemisiae*, n. sp. (squares), *middlekauffi* Alexander (circle) and *woodi* Alexander (triangles).



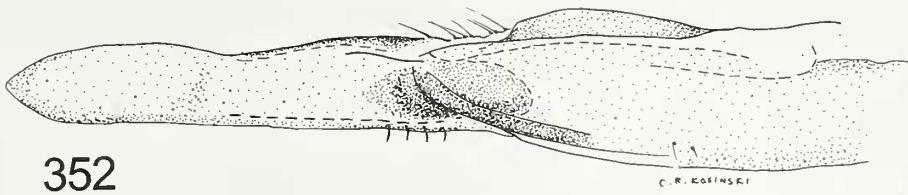
Figs. 332–338. *Tipula* (*Eremotipula*) *middlekauffi*, male. 332, 333, ninth tergum, dorsal and ventral views. 334, outline of dorsal lobes and subtergal process of ninth tergum, right ventral lobe also shown, holotype. 335, appendage of ninth sternum, lateral view, holotype. 336, inner dististyle, lateral view. 337, adminiculum, dorsal view. 338, membranous lobe, inner view, holotype. Scale a: 332–333, 337; b: 334, 336; c: 335, 338.



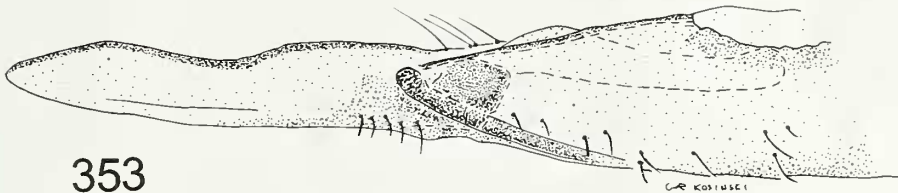
Figs. 339–348. *Tipula (Eremotipula) sinistra*, male. 339, 340, ninth tergum, dorsal and ventral views. 341, ventral lobe of ninth tergum. 342, appendage of ninth sternum, posterolateral view. 343, abdominal segment 1 showing elongate setae, lateral view. 344, 345, inner dististyle, lateral and dorsal views. 346, 347, adminiculum, lateral and dorsal views. 348, sclerotized apical border of eighth sternum. Scale a: 343, 348; b: 339–341, 345, 347; c: 344, 346; d: 342.



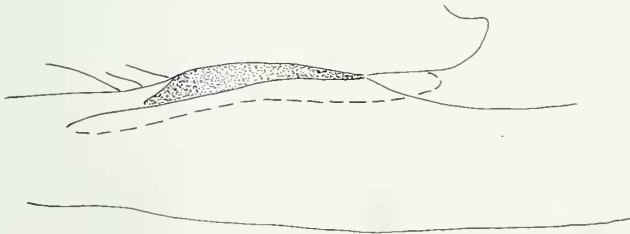
Figs. 349–351. *Tipula* (*Eremotipula*) *sinistra*, male. 349, outer dististyle, lateral view. 350, apex of eighth sternum. *lat. scl.* = lateral sclerite, *mbl* = membranous lobe. 351, detail of membranous lobe of eighth sternum. Scale a: 350; b: 349; c: 351.



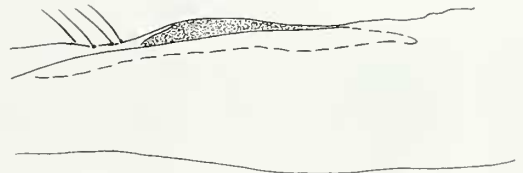
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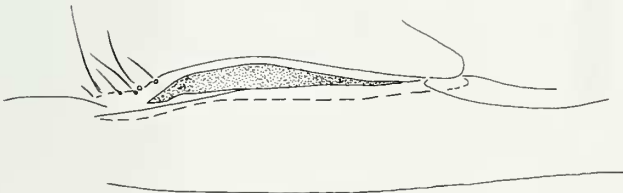
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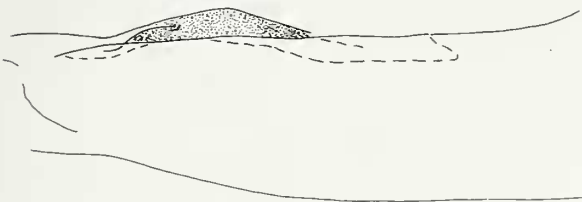
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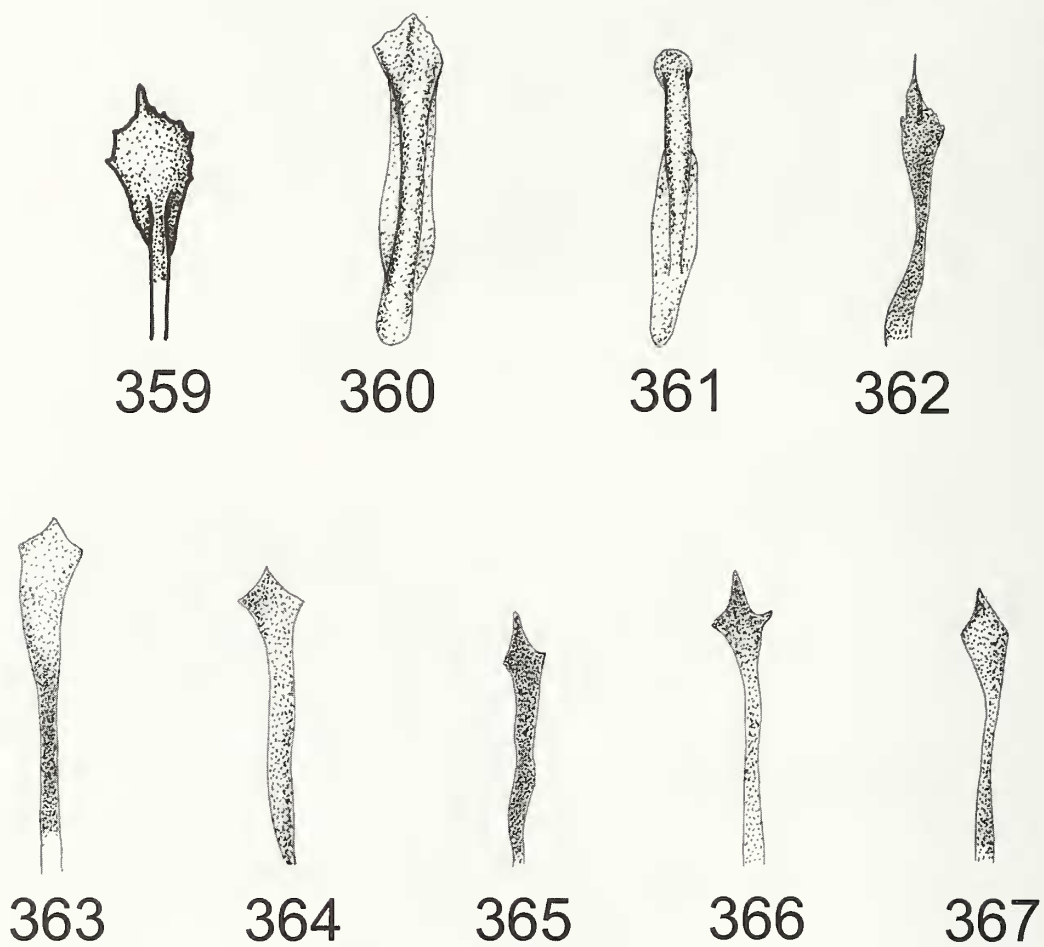


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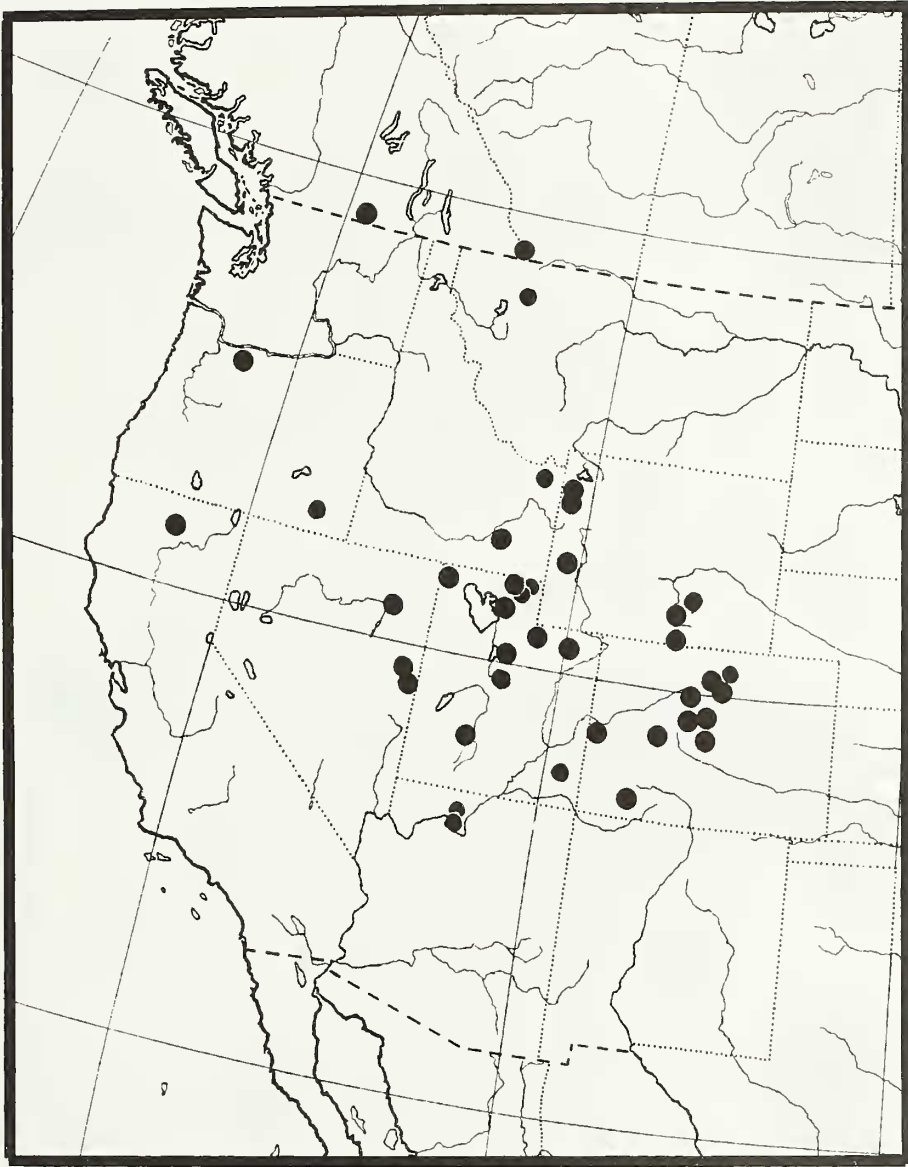


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Figs. 352–358. *Tipula* (*Eremotipula*) *sinistra* group females. 352–353, lateral view of eighth sternum and hypogynial valve. 352, *sinistra*, Nevada: Elko Co. 353, *woodi*. 354–358, *sinistra*, inner ridge, lateral view. 354, Alberta. 355, Wyoming: Carbon Co. 356, Colorado: Larimer Co. 357, Utah: Cache Co. 358, Arizona: Coconino Co.

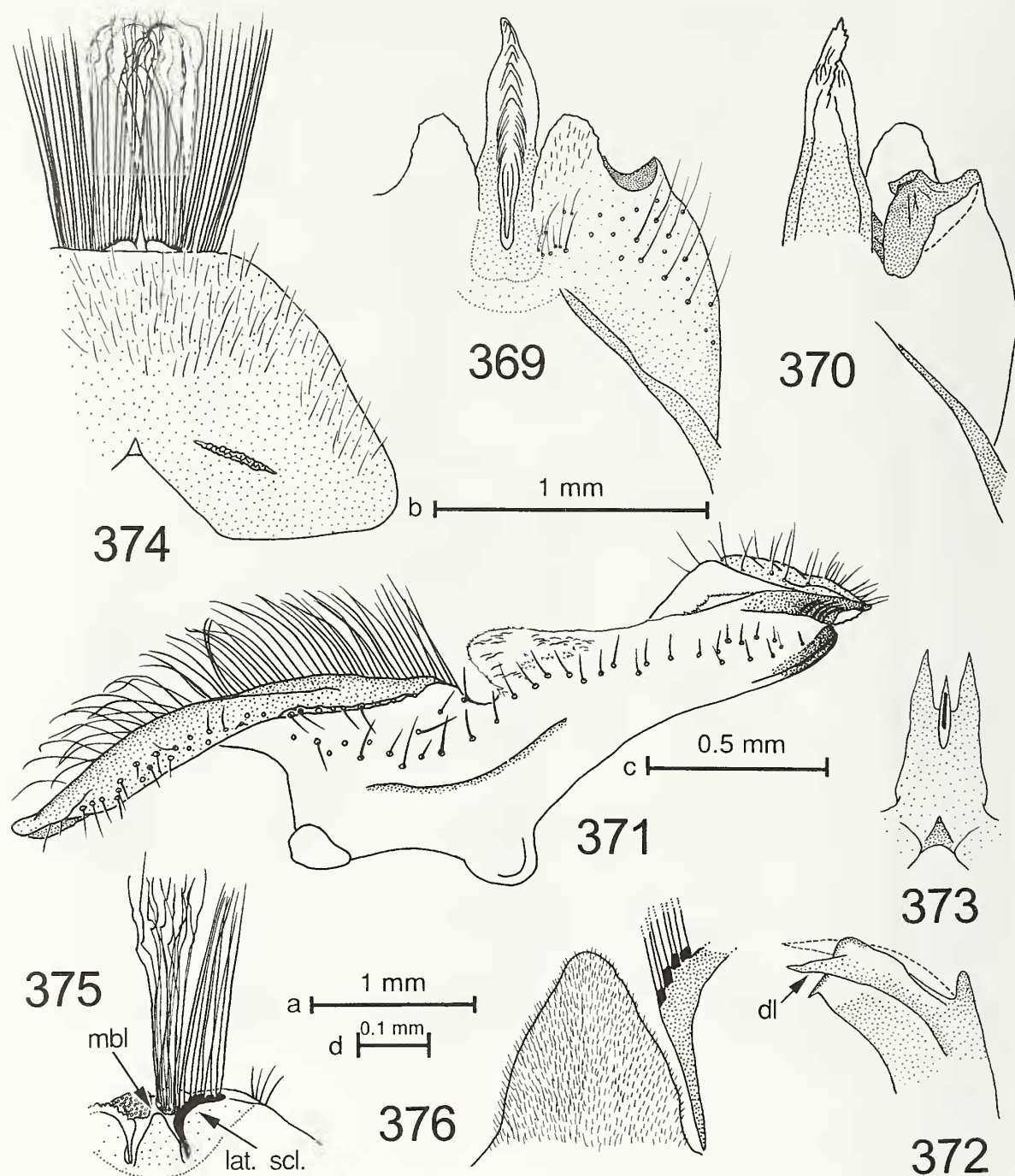


Figs. 359–367. *Tipula* (*Eremotipula*) spp., female, vaginal apodeme. 359, *jicarilla*. 360, 361, *lyrifera*. 362, *woodi*. 363–367, *sinistra*.

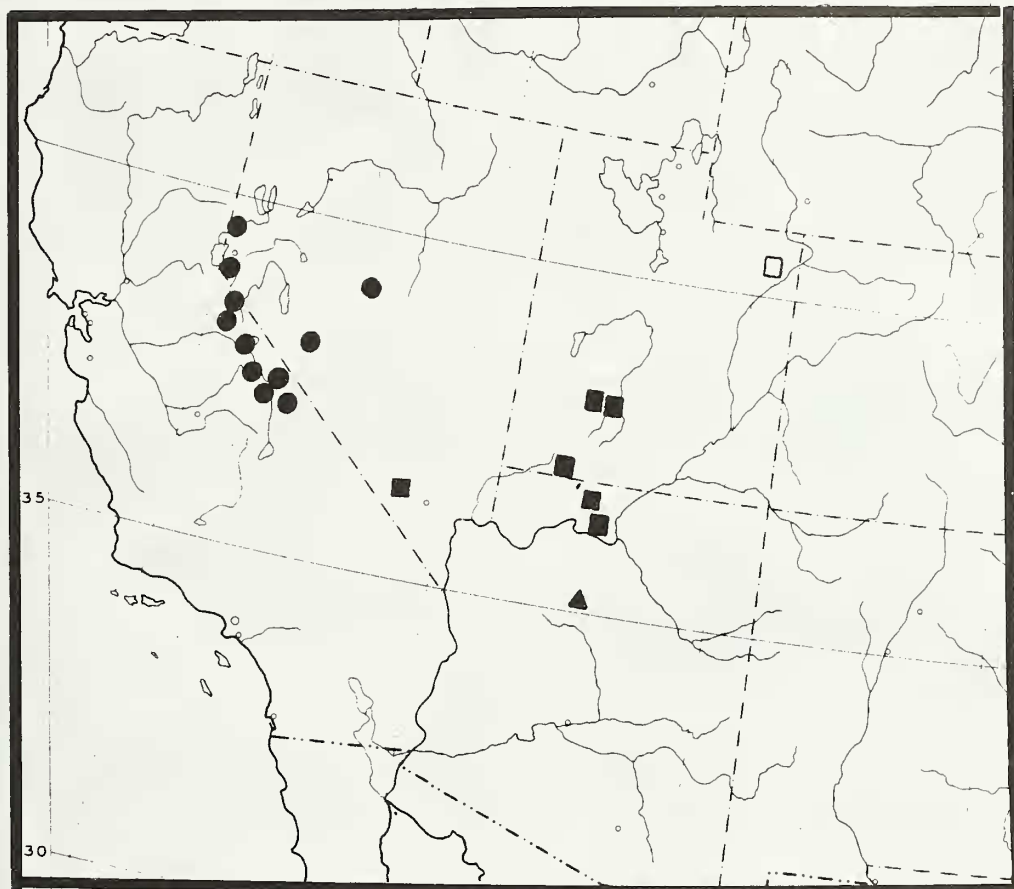


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Fig. 368. Distribution of *Tipula (Eremotipula) sinistra* Dietz.

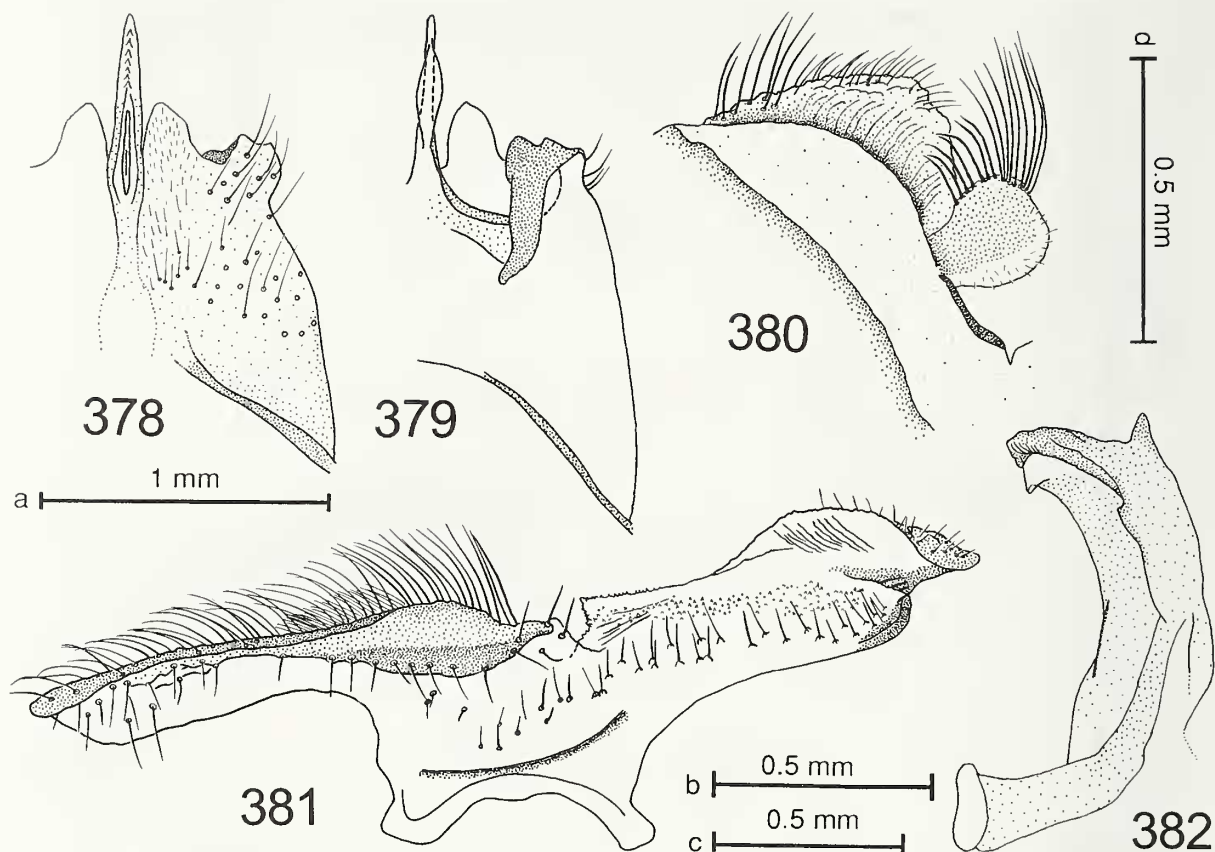


Figs. 369–376. *Tipula* (*Eremotipula*) *dissipina*, male. 369, 370, ninth tergum, dorsal and ventral views. 371, inner dististyle, lateral view. 372, 373, adminiculum, lateral and dorsal views. 374, 375, eighth sternum, inner and outer views. *lat. scl.* = lateral sclerite, *mbl* = membranous lobe. 376, membranous lobe of eighth sternum, inner view. Scale a: 374–375; b: 369–370, 372–373; c: 371; d: 376.

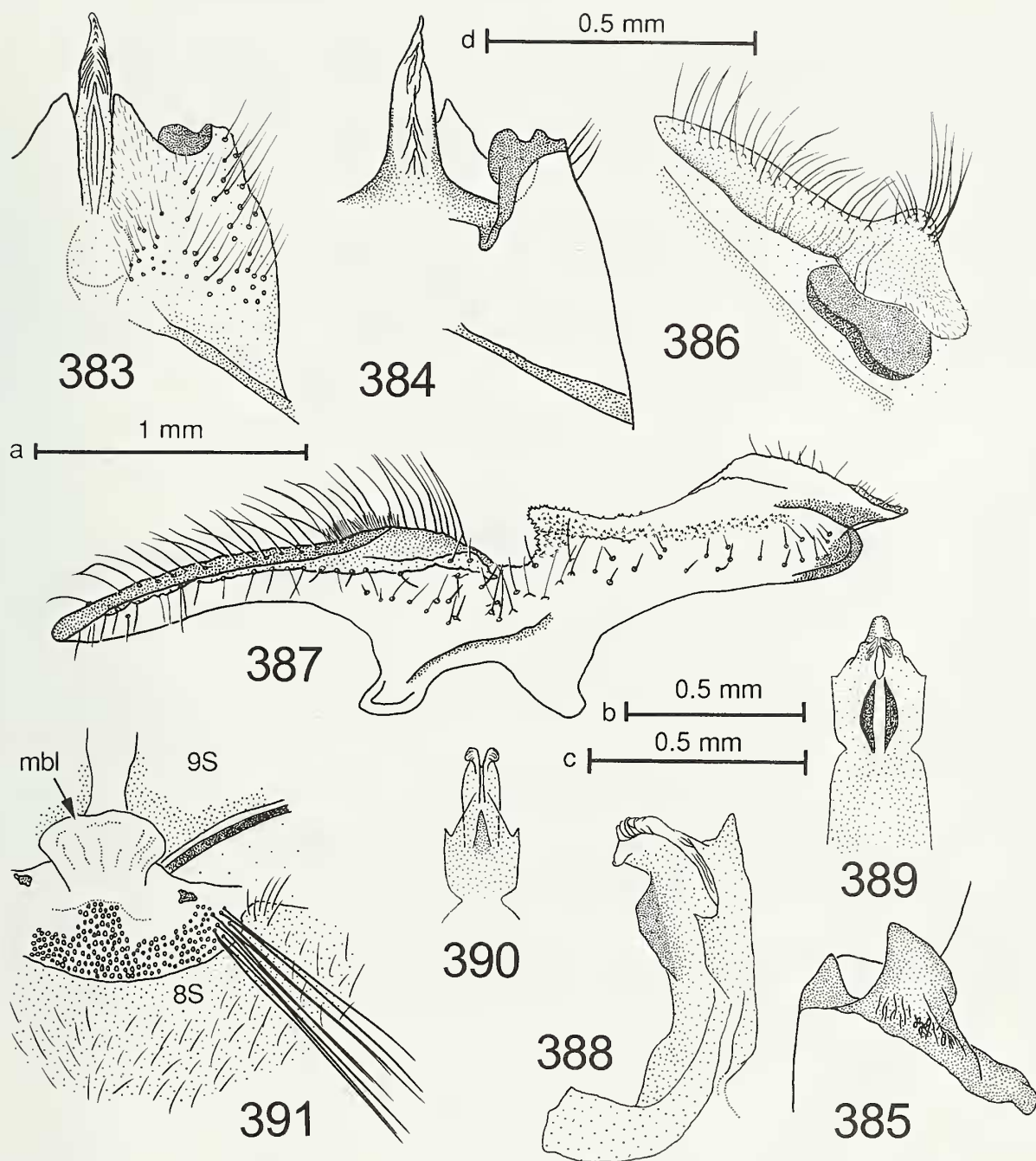


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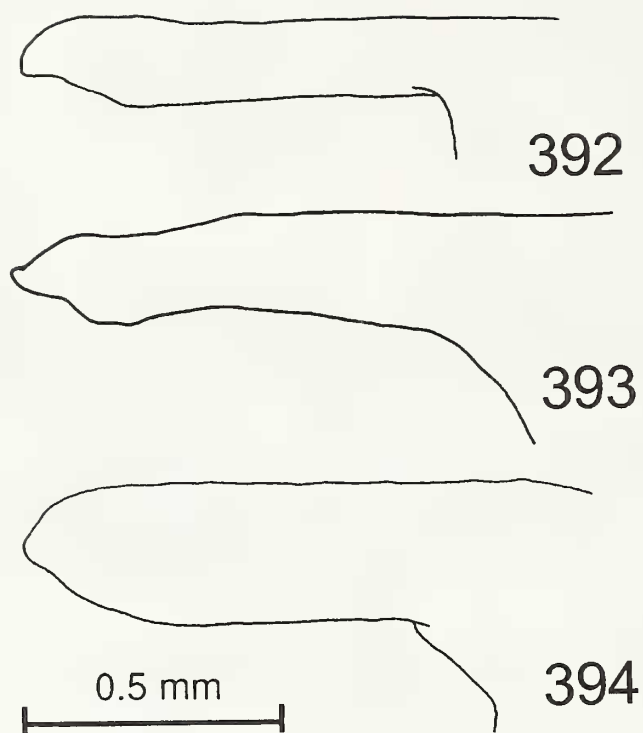
Fig. 377. Distributions of *Tipula (Eremotipula) dissipina*, n. sp. (triangle), *evalynae*, n. sp. (squares) and *leioantha* Alexander (circles). The open square represents a county locality without further data.



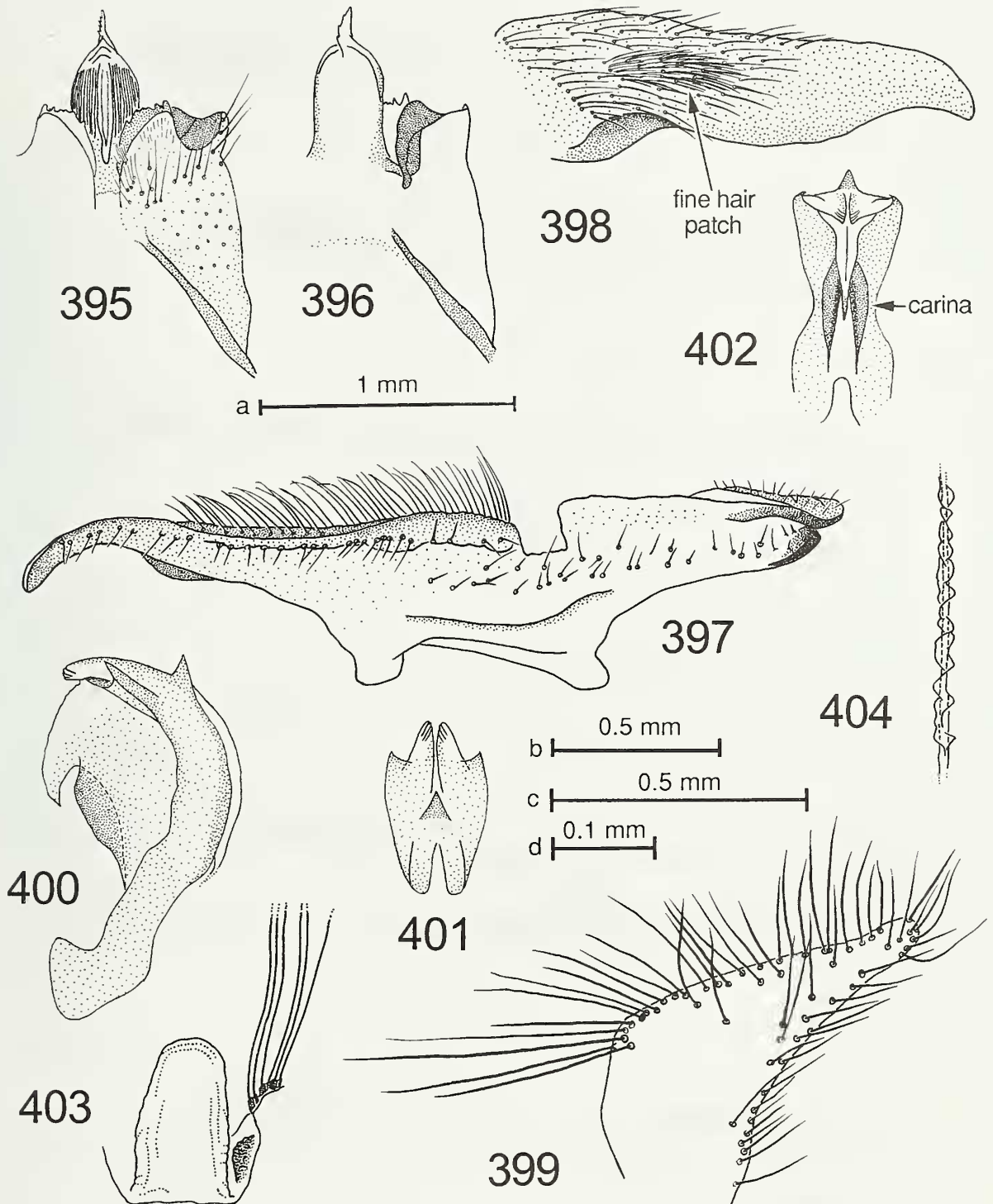
Figs. 378–382. *Tipula (Eremotipula) evalynae*, male. 378, 379, ninth tergum, dorsal and ventral views. 380, appendage of ninth sternum, lateral view. 381, inner dististyle, lateral view. 382, adminiculum, lateral view. Scale a: 378–379; b: 380; c: 381; d: 382.



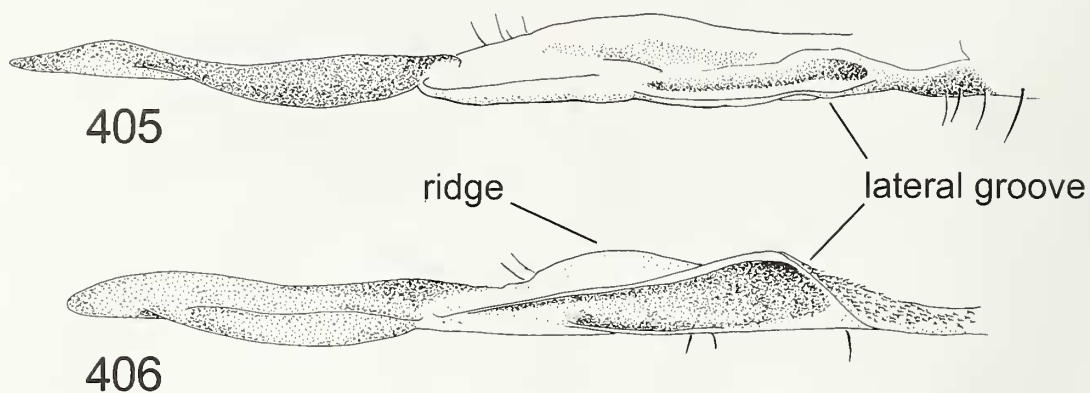
Figs. 383–391. *Tipula (Eremotipula) leiocantha*, male. 383, 384, ninth tergum, dorsal and ventral views. 385, detail of ventral lobe of ninth tergum, holotype. 386, appendage of ninth sternum, lateral view. 387, inner dististyle, lateral view. 388–390, adminiculum, lateral, posterior and dorsal views. 391, intersegmental region between eighth and ninth sterni (half shown only, most setae omitted). *mbl* = membranous lobe. Scale a: 383–384, 389–391; b: 387–388; c: 386; d: 385.



Figs. 392–394. *Tipula* (*Eremotipula*) *leiocantha*, outer basal lobe of inner dististyle, outline of mesal view. 392, holotype. 393, paratype. 394, California: Mono Co., Coleville.

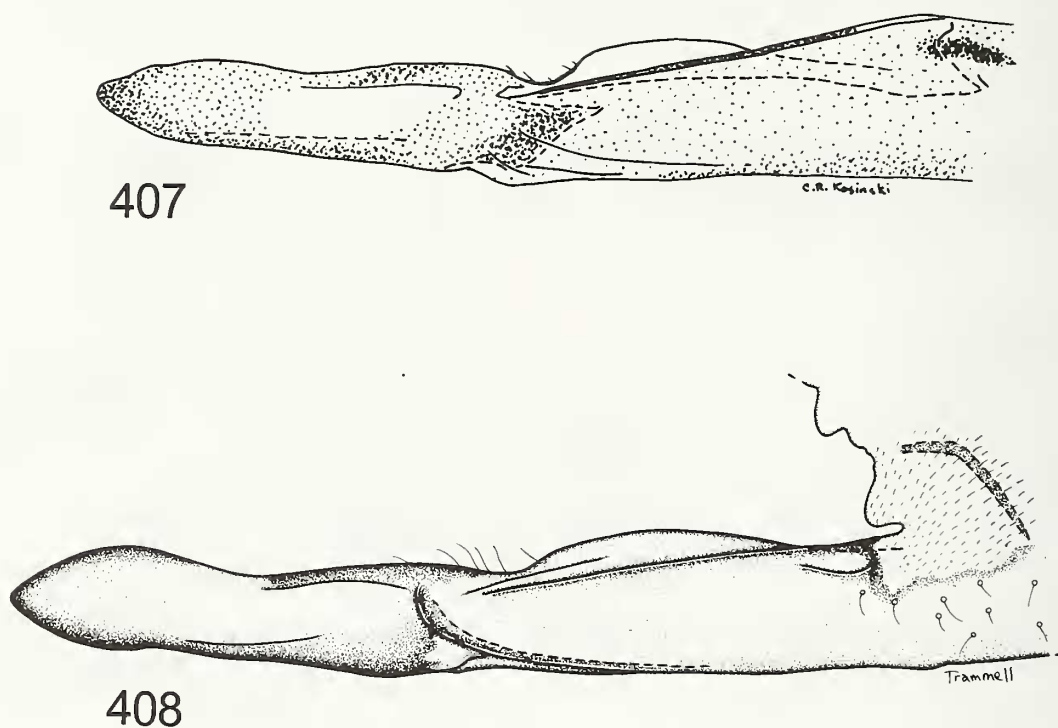


Figs. 395–404. *Tipula (Eremotipula) lyrifera*, male. 395, 396, ninth tergum, dorsal and ventral views. 397, inner dististyle, lateral view. 398, outer basal lobe of ID, mesal view. 399, outer dististyle, lateral view. 400–402, aedeagus, lateral, posterior and dorsal views. 403, membranous lobe of eighth sternum, inner view. 404, carinate setae of eighth sternum. Scale a: 395–398, 401–402; b: 400, 403; c: 399; d: 404.

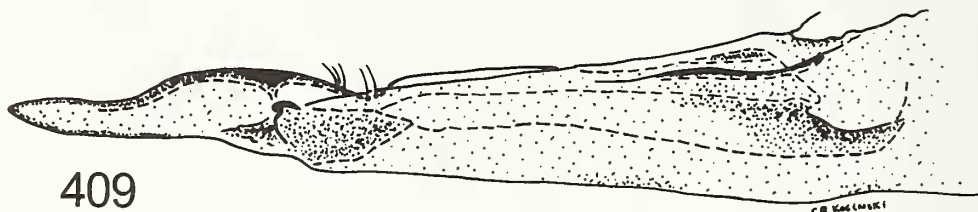


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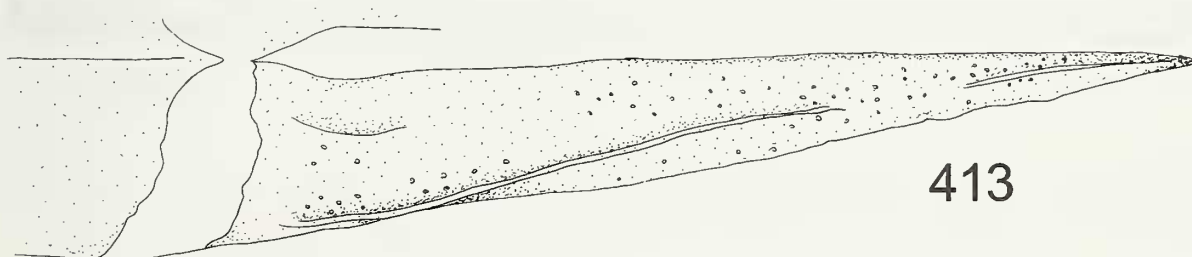
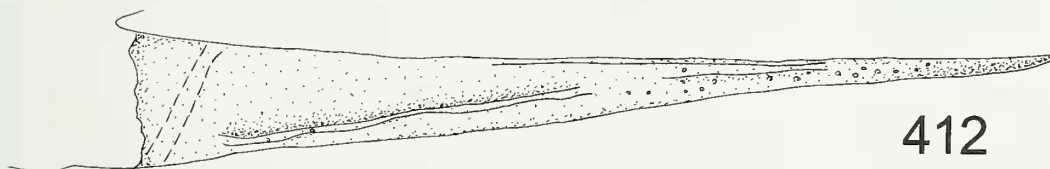
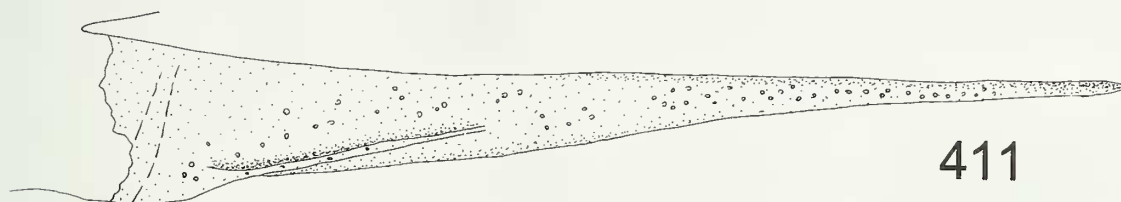


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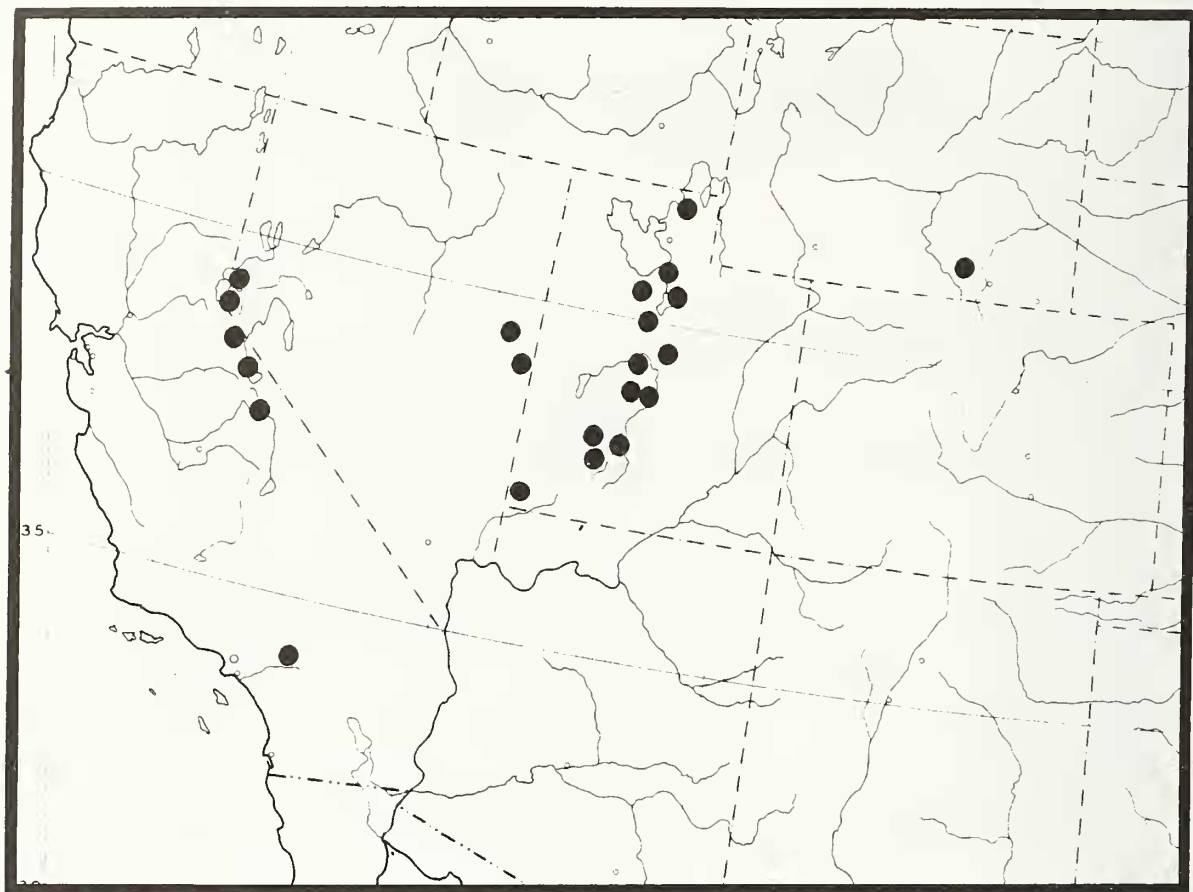


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Figs. 405–409. *Tipula* (*Eremotipula*) *diversa* group females, eighth sternum and hypogynial valve. 405, *sackeni*, dorsal view. 406, 407, *diversa*, dorsolateral view. 408, *evalyinae*, lateral view. 409, *lyrifera*, lateral view.

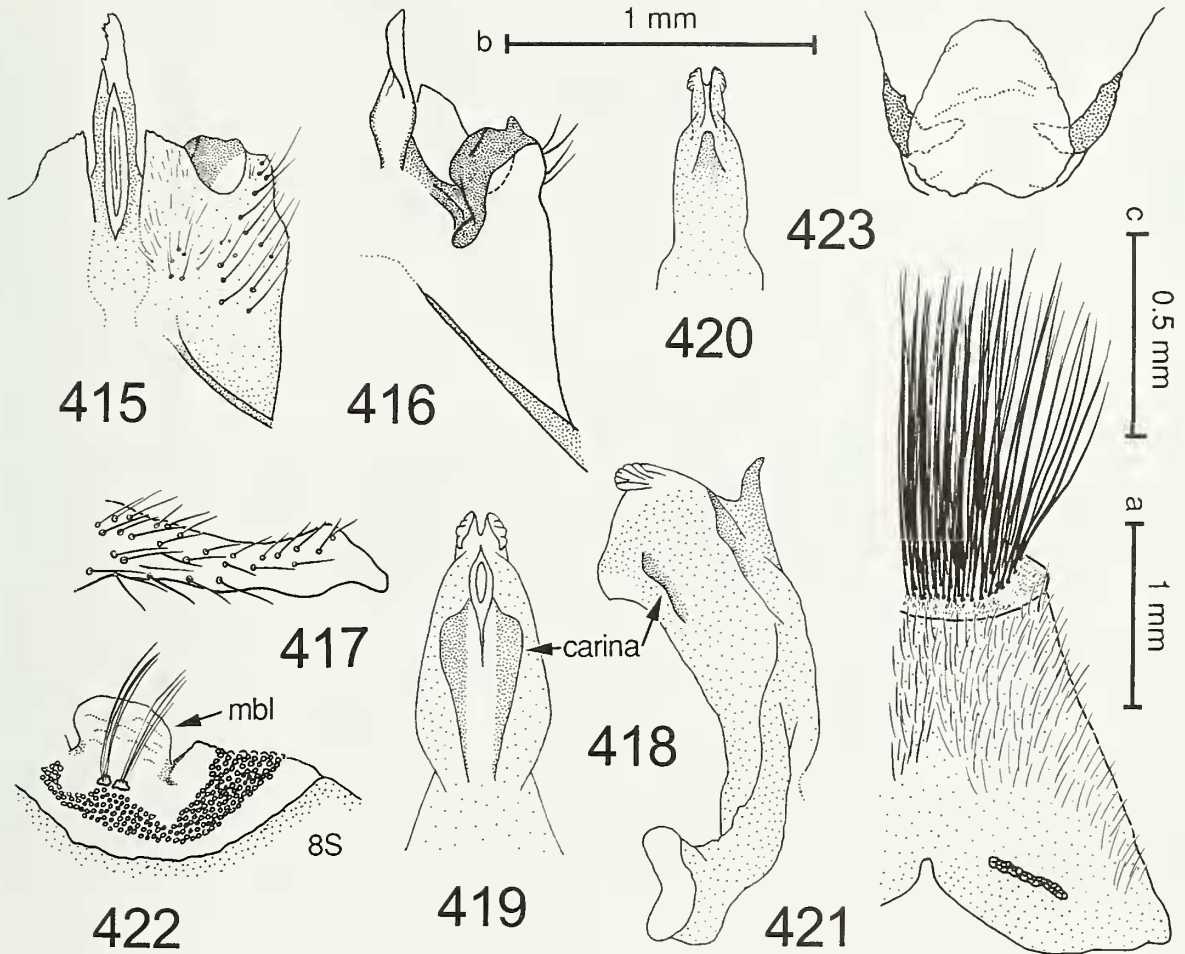


Figs. 410–413. *Tipula* (*Eremotipula*) *diversa* group females, cerci, dorsal view (left half drawn). 410, *leiocantha*. 411, *diversa*. 412, *evalynae*. 413, *lyrifera*.

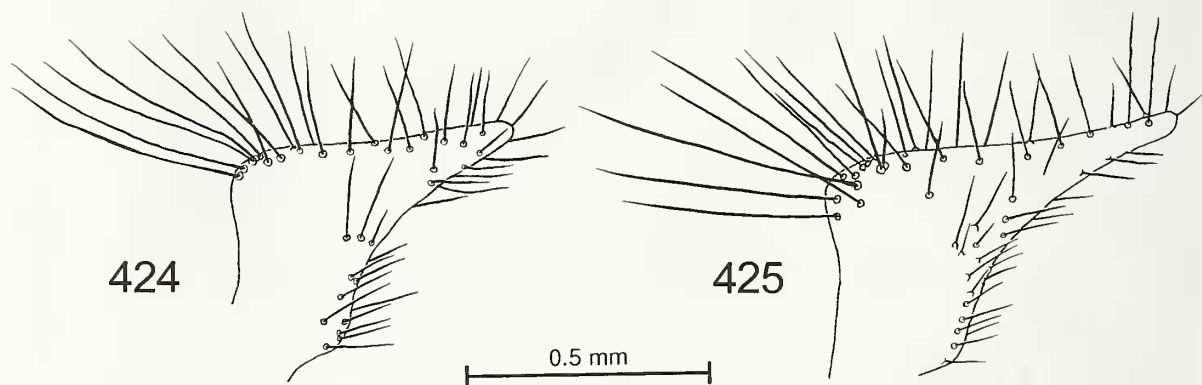


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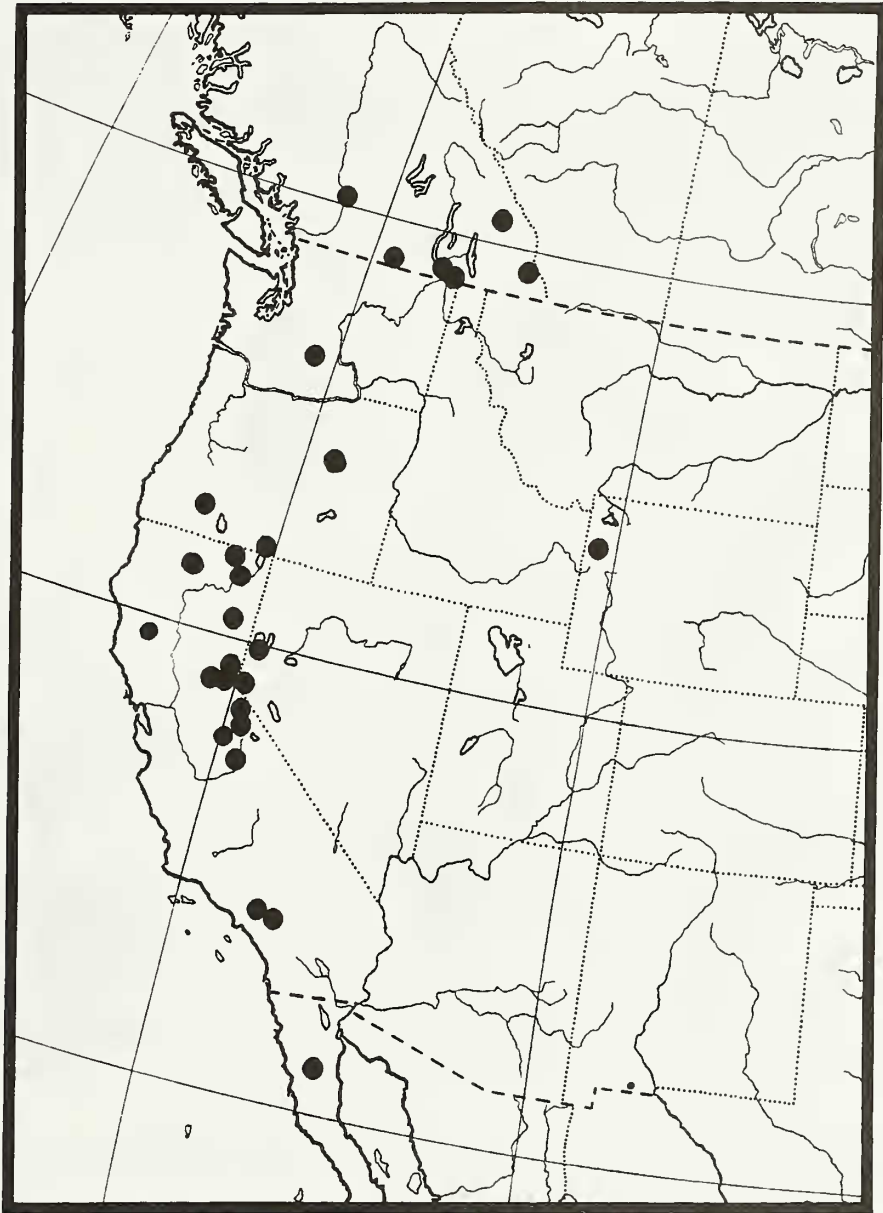
Fig. 414. Distribution of *Tipula (Eremotipula) lyrifera* Dietz.



Figs. 415–423. *Tipula (Eremotipula) sackeni*, male. 415, 416, ninth tergum, dorsal and ventral views. 417, outer basal lobe of ID, mesal view; California: Mono Co. 418–420, adminiculum, lateral, posterior and dorsal views. 421, eighth sternum. 422, apex of eighth sternum (showing isolated setal groups). *mb* = membranous lobe. 423, membranous lobe of eighth sternum, inner view. Scale a: 421; b: 415–416, 422; c: 417–420, 423.

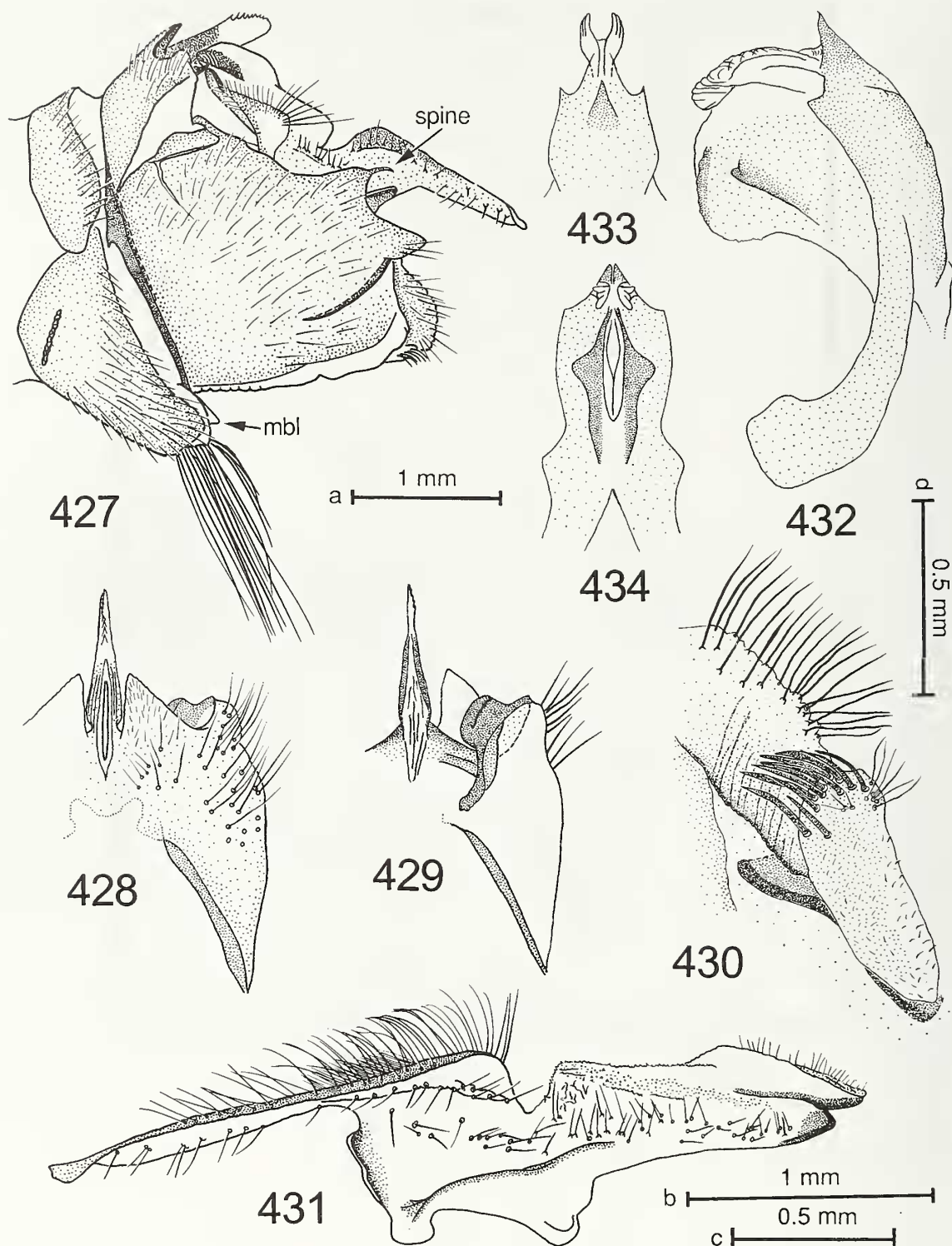


Figs. 424–425. *Tipula* (*Eremotipula*) *sackeni*, outer dististyle, lateral view. 424, California: Mono Co. 425, California: Los Angeles Co.

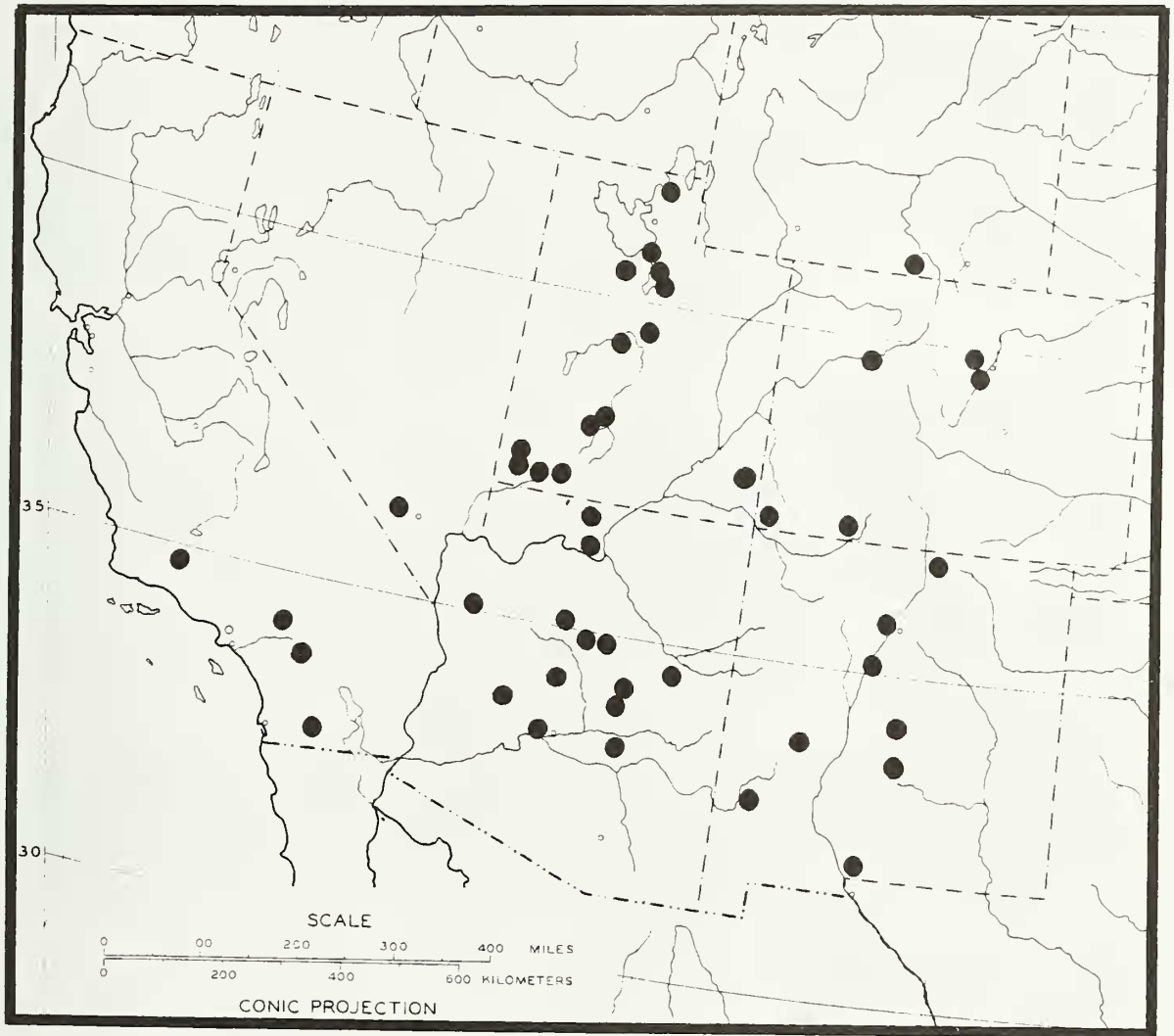


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Fig. 426. Distribution of *Tipula (Eremotipula) sackeni* n. sp.



Figs. 427–434. *Tipula (Eremotipula) diversa*, male. 427, male hypopygium, lateral. *mbl* = membranous lobe. 428, 429, ninth tergum, dorsal and ventral views. 430, appendage of ninth sternum, dorsolateral view. 431, inner dististyle, lateral view. 432–434, adminiculum, lateral, dorsal and posterior views. Scale a: 427; b: 428–429, 431, 433–434; c: 432; d: 430.



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Fig. 435. Distribution of *Tipula (Eremotipula) diversa* Dietz.

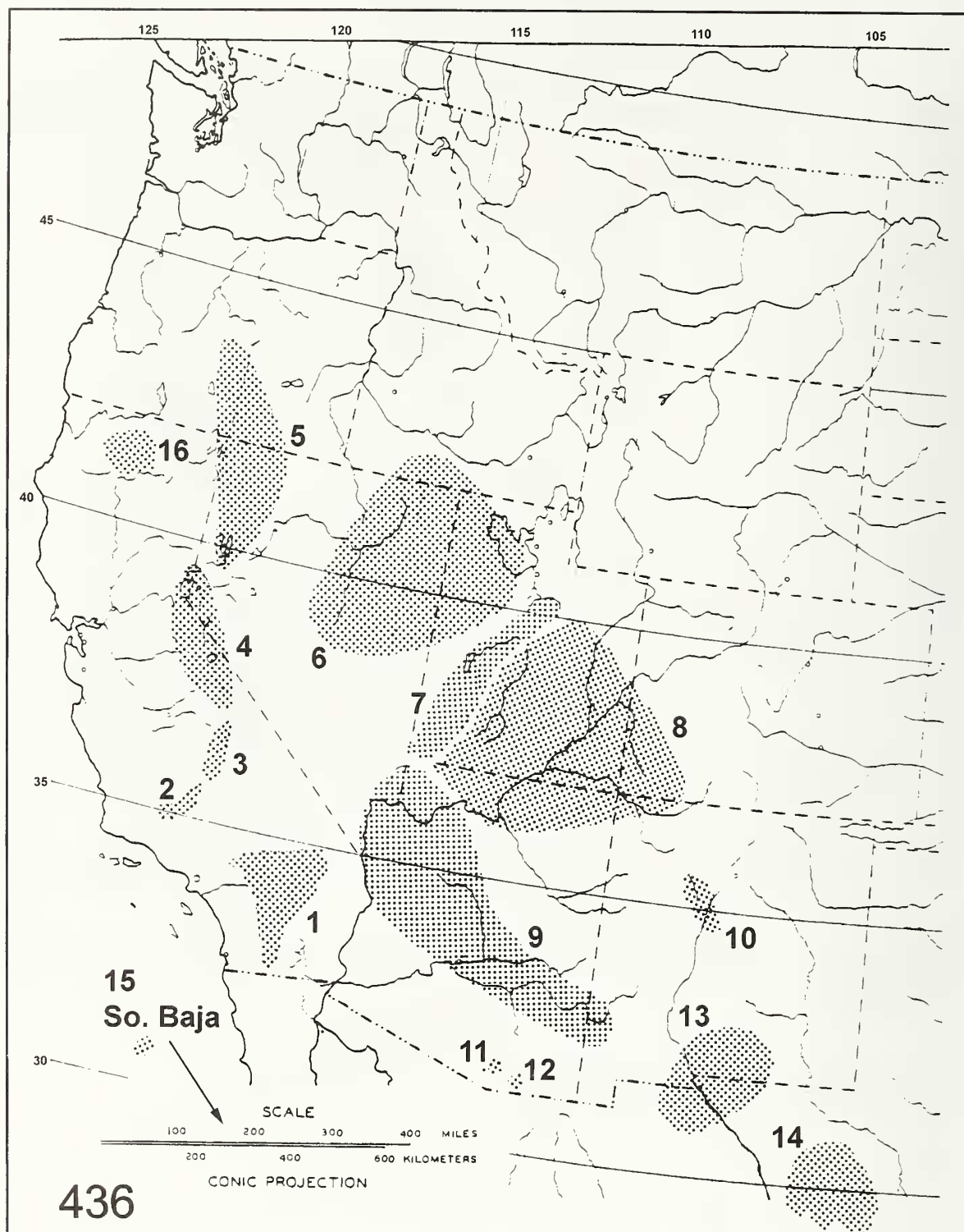
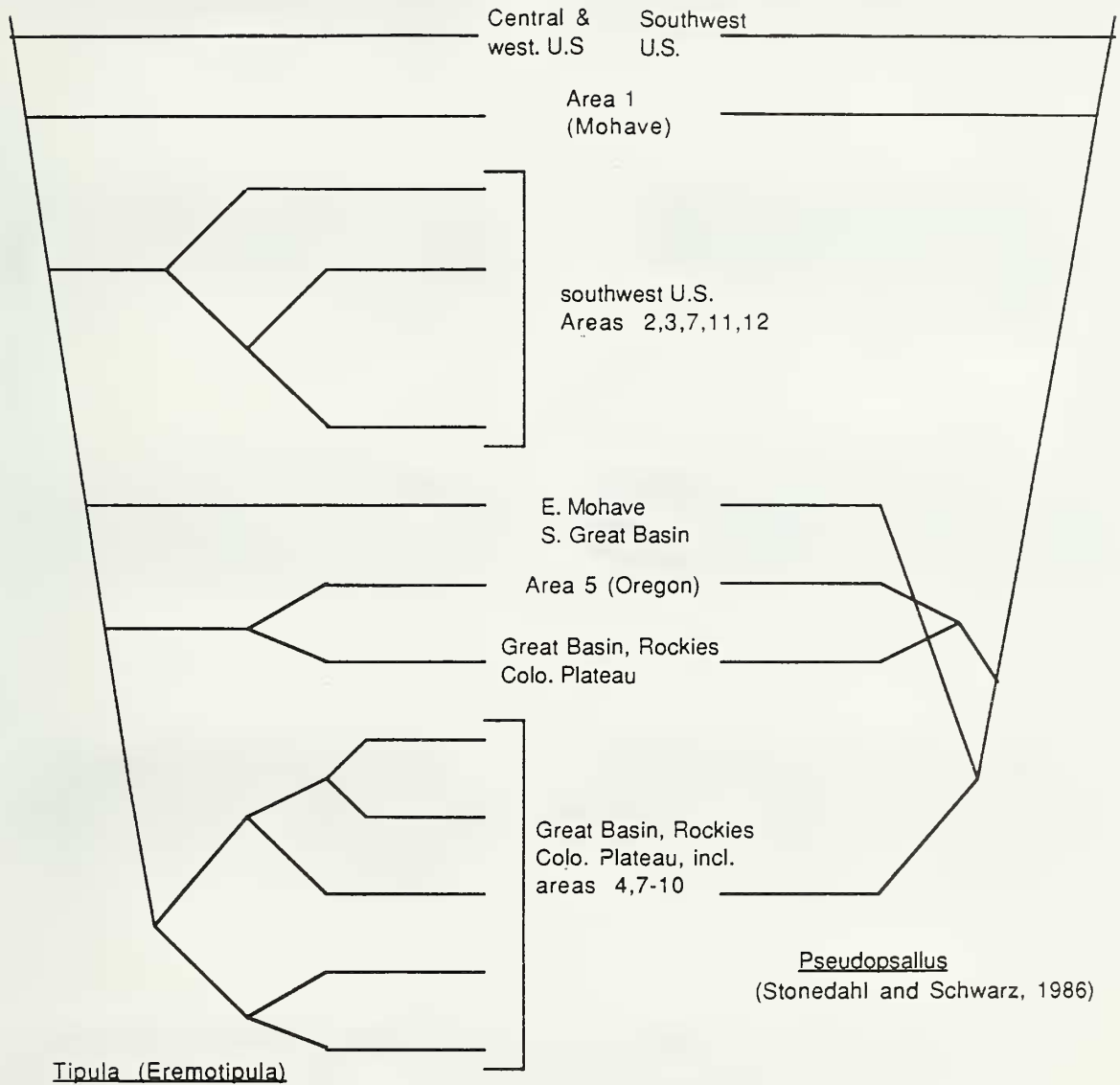


Fig. 436. Areas of endemism for species of *Tipula* (*Eremotipula*) and some arid land *Tipula* (*Lunatipula*) s.str. species groups. Areas 1-12 supported by species of *Eremotipula*. See Table 7 for list of species per area.



Lineage lines represent one or more species.

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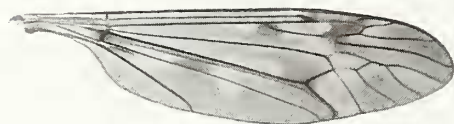
Fig. 437. Congruence of area cladograms of *Tipula (Eremotipula)* and *Pseudopsallus* (Hemiptera). Cladogram for *Eremotipula* based on Fig. 21.



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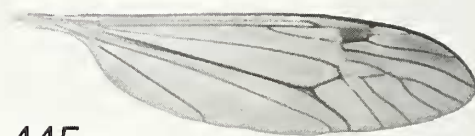
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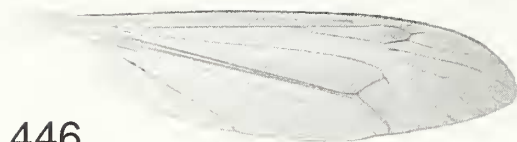
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Figs. 438–441. Wings of *Tipula* (*Eremotipula*). 438, *incisa*, male. 439, *incisa*, male, "*ericensis* form". 440, *incisa*, male, "*picturata* form". 441, *incisa*, male, "*queres* form".



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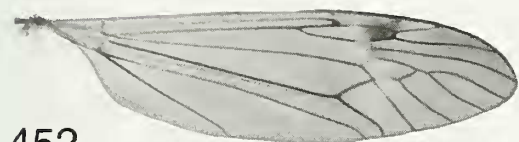
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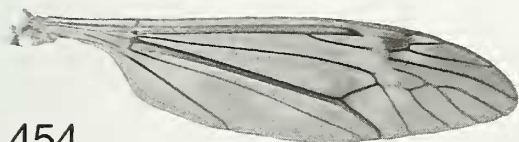
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Figs. 442–445. Wings of *Tipula* (*Eremotipula*). 442, *kirkwoodi*, male. 443, *pellucida*, female. 444, *helferi*, male. 445, *spinerecta*, male.